LEAF-MINING INSECTS

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By

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*"There's never a leaf nor blade too mean
To be some happy creature's palace."*

J. R. Lowell, VISION of SIR LAUNFAL.

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PREFATORY NOTE BY THE SENIOR AUTHOR

Something should be said in explanation of the part that has been taken by each of the authors in the preparation of this book. It was begun under my direction by Miss Hughes, now Mrs. John D. Tothill, when she was a graduate student in my laboratory at Cornell University. It was continued by her subsequently in Illinois, Wisconsin, British Columbia, and especially at Frederickton, New Brunswick.

Meanwhile, Dr. Frost had begun the study of leaf-miners at Cornell University under the direction of Dr. R. Matheson.

When Mrs. Tothill was preparing to go with her husband on an important scientific mission to the Fiji Islands (where she has been during the final putting together of this book) she appealed to me to find some means of completing it. I, naturally, turned to Dr. Frost, and we agreed to complete it together.

My own part has been chiefly that of editing and writing introductions, though I have contributed some notes and illustrative material from my own rearings in each of the four orders of leaf-miners. Dr. Frost has written the chapter on Dipterous miners and has compiled the bibliography and the tables of species and food plants for all four orders. We have worked together on most of it.

At the end of it we are all under obligation for help to more people than we can now name. We are all indebted first of all for generous and oft-repeated aid with the Lepidoptera to Dr. W. T. M. Forbes; likewise, with other orders, to Dr. R. Matheson. Mrs. H. E. Seemann has been very helpful in arranging the illustrations. I have been aided in the collecting and preparation of materials by Miss Anne Snitow and Miss Helen Albro. Mrs. Tothill has had the aid of her husband, Dr. John D. Tothill, and of Mr. W.

Downes and Mr. Treherne of the Canadian Dominion Entomological Service. Dr. Frost wishes to acknowledge help in the determination of specimens from Dr. J. M. Aldrich, Dr. Adam Boeving and Mr. S. A. Rohwer, all of the U. S. National Museum.

I, as senior author, wish to assume responsibility for the omission of the name of the describer of the species after each scientific name.

Our undertaking has been threefold. We have endeavored to provide (1) an untechnical introduction to the study of leaf-mining insects, intelligible to the general reader; (2) an account of their natural history sufficiently detailed to be useful to the working ecologist; and (3) lists of the leaf-miners, of their food plants, and of technical papers concerning them adequate for the needs of the specialist. Thus we have undertaken to make more available to students, the rich but hitherto widely scattered results of many excellent investigations in this interesting ecological field.

Here there is much that should be of interest to the general biologist. The mandibulate leaf-mining larvae show a convergence in form that is almost without a parallel elsewhere. They also present an unique example of hypermetamorphosis that hitherto has been almost or quite ignored by all the text books in their discussions of that subject. Leaf-mining moth larvae are not ordinary caterpillars; at least, the sap-feeders are not. The mouthparts they have developed for shearing and sap drinking and the form of head associated therewith are quite their own.

Any one with a taste for natural history will find interest in observing how these tiny creatures get their living, find their shelter, keep their dwelling places clean and sanitary, provide for all the shifts of stage and station, and manage the ordinary business of their lives. Their ways are quite unique in the animal world.

JAMES G. NEEDHAM.

Ithaca, April 20, 1926.

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CHAPTER I

A General Acquaintance with Leaf-mining Insects

Green leaves are the world's dependence for food production. Day by day, as the sun shines on them they build up the organic substances by which all men and all animals live. Directly or indirectly they feed both great and small. Their consumers range in size from the great elephants of the tropical jungle down to the little tenants of single leaves that are the subject of this volume.

Leaf-miners are among the smallest of plant-eating animals. Most of them find both sustenance and shelter within the confines of a single leaf—often within a small portion of a leaf, between its upper and its nether epidermis. Their food is the thin stratum of green tissue that lies, like coal in a mine, outspread in a seam between two worthless adjacent strata, and the insects get it and dig it out for use. That is why we call them miners.

Leaf-miners are everywhere. In any lane or fence-row they may be found by one who will take the trouble to look for them. Their signatures, written in the leaves, are plainly outspread to view. The foliage of almost any oak tree or hornbeam or clump of goldenrod will show in autumn the characteristic marks of several kinds of them.

Some of them make winding galleries like that of the little fly in the aster leaf shown in figure 1, and when grown leave the leaf through a slit in the epidermis and enter the soil to undergo their transformations. Others excavate broader chambers within the leaf, and remain inside them to transform. The mothlet whose mine is shown in figure 2 is of the latter habit. It makes a broad mine in a lobe of a leaf of the white oak. It disposes of its waste in a corner

of the mine, stowed away behind a screen of white silk. When grown it spins a filmy cocoon of silk, moored to the walls with radiating stay lines of the same material, and

FIG. 1. Leaf of the white aster, *Aster paniculatus*, with a mine of the fly *Phytomyza albiceps*.

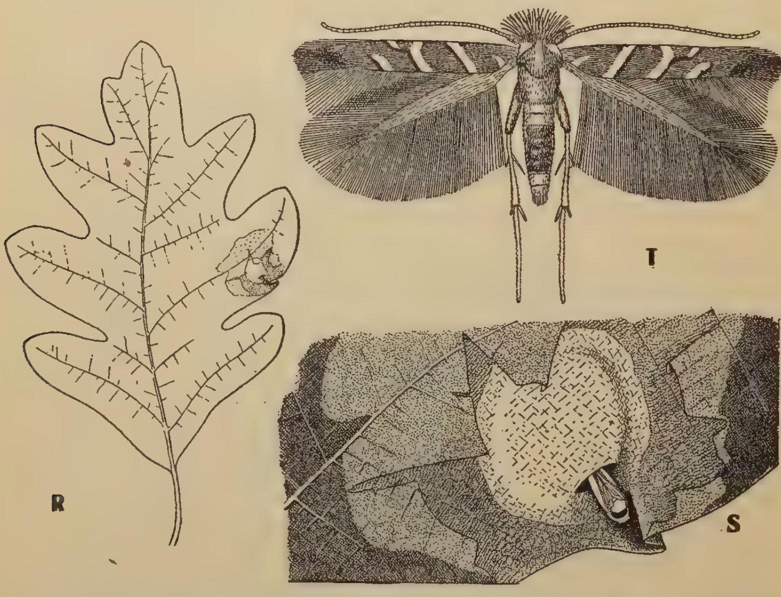


FIG. 2. The white oak leaf-miner *Lithocolletis hamadryadella*. *R*, a leaf of white oak bearing a ruptured mine; *S*, the mine enlarged showing the empty chrysalis protruding; *T*, the adult moth. (Drawn by C. H. Kennedy.)

within this it transforms to a pupa. The pupa has a sharp hornlike process on its head with which, when ready for the final transformation, it can penetrate the walls. When

part way out of the leaf the pupal shell (chrysalis) breaks open on the back, and from it emerges a resplendent little moth, clad in scales of gold and ermine and jet, a veritable atom of Lepidopterous loveliness.

There is hardly anything in nature more beautiful than are some of the moths that have leaf-mining larvae.

THE LEAF AS A DWELLING PLACE

The leaf is a peculiar place in which to live. As every one knows, it is merely an expansion of the plant body containing green cells thinly outspread for advantageous exposure to the light. A leaf consists essentially of this layer of assimilatory cells, covered by and enclosed in a transparent epidermis, and supported by a framework of veins. It is generally, but not always flat, and it varies enormously in details of form, size, structure and content, each species of plant producing leaves after its own kind. We must have the common characteristics of leaves in mind if we would understand the operations of the insects that dwell in them.

The *epidermis* is primarily a protective outside layer. It protects the soft semiliquid protoplasmic cells of the parenchyma from evaporation, and to some extent also from destruction by foraging animals. It consists generally of a single layer of rather thick walled transparent cells, covering the entire leaf and continuous with the epidermis of the stem. It is perforated by pores or stomates that facilitate the intake of carbon dioxide from the air and the outgo of watery vapor. Each stomate is bordered by two guard cells, that automatically regulate transpiration, by opening when moisture is abundant and closing when it is scanty. The guard cells, unlike most other epidermal cells, contain green chlorophyl bodies. Often the cells of this epidermal layer secrete on the outside a common cuticle, that is highly protective and waxy, or varnish-like exuda-

tions are sometimes added upon its surface. Plant hairs are commonly developed from single cells of the epidermis, more abundantly, as a rule, upon the lower surface of the leaf.

Midrib and veins have a twofold function in the leaf. They contain hard parts that make them supporting structures, and they contain the vessels that are the channels of circulation within the plant, bringing up water with its content of mineral salts from the ground, and taking to other parts of the plant the sugars and other products of assimilation that are manufactured in the leaves. In so far as the veins contain cells having hard walls, they offer an impediment to the work of the leaf-miners.

The part of the leaf for which all other parts exist and on whose products all other parts of the plant subsist, is the soft living, protoplasmic, chlorophyl-containing parenchyma. This is variously disposed in different types of leaves, but in general it tends to be differentiated into two layers: a *palisade layer* of one or more rows of closely placed, usually columnar cells next the epidermis, and a *spongy layer* of irregularly placed and openly spaced cells beneath or within. The stomates of the epidermis open into the interspaces between the cells of the spongy layer.

It is a part of the fitness of things that the close packed palisade cells, with their rich content of chlorophyl should be placed directly in contact with the transparent upper epidermis of the leaf where they are reached by effective light; and that stomates should be relegated mostly to the lower epidermis where they control the admission of air to the moist chamber of the spongy parenchyma, maintaining proper conditions there for the exchange of gases in metabolism. The palisade layer is the chief seat of food production. It is the part of the leaf that is sought out by the more specialized leaf-miners: the lower, more easily penetrable, spongy layer is the first sought by the unspecialized.

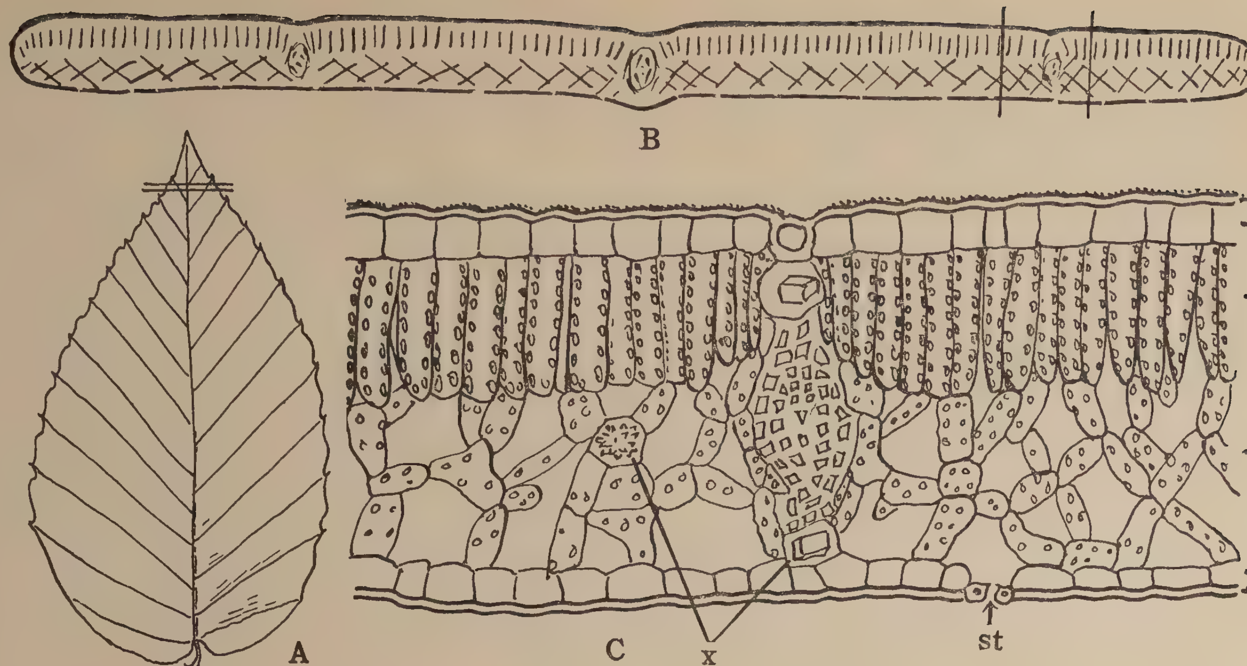


FIG. 3. Diagrams of leaf structure. *A*, a birch leaf; *B*, a cross-section of same at the point indicated by the parallel cross-lines in *A*; *C*, a magnified bit from *B*; *c*, *c*, cuticle; *e*, *e*, epidermis; *p*, palisade layer of the mesophyll; *s*, spongy layer; *v*, veinlet; *x*, mineral crystals; *st*, stoma.

In so far as the work of these insects is concerned, we may regard the tissues in the leaf of two sorts, one of which is eaten and one is not. The latter is the epidermis with its cuticle.[1] The other, whether parenchyma or vein, or both, we may for practical purposes designate as *mesophyll*.

THE INSECTS

Leaf-miners are all larvae. No adult insects have been able to establish themselves in such a habitat. It is only the worm-like, quick-growing young of those groups of insects which have complete metamorphosis with both larval and pupal stages in their life cycle, those that feed extensively on plants, and are very small in size, that have become leaf-miners. They are the larvae of four great groups, which, named in the order of their importance are:

1. Caterpillars or moth larvae; order Lepidoptera
2. Grubs or beetle larvae; order Coleoptera
3. Maggots and other two-winged fly larvae; order Diptera
4. Sawfly larvae; order Hymenoptera.

These are the same four orders that everywhere are the world's keenest competitors for food, and that make up the bulk of the animal population.

The pressure for room and for sustenance has been very great and all kinds of shifts for a living have been tried; and these little fellows have shifted into the interior of leaves where the mesophyll provides abundant food, and the epidermis is their shelter.

The adults of these four orders are very unlike; moths and beetles and true flies, and sawflies. No one would imagine that they could come from larvae that seem so nearly alike. Every one who has studied leaf-miners is at once struck by this similarity of larvae. It is a remarkably good illustration of the moulding power of environment. Within the leaf the conditions are alike for all, and all have been moulded

[1] In descriptions sometimes mentioned by either name.

to a common form. While all larvae are more or less worm-like, the free-living ones are easily referable to their orders but it is often difficult for a good entomologist to tell whether the creature he has found mining a leaf is the larva of a moth, a beetle, or a sawfly.

This is true of the more specialized forms only. In each order there are leaf-miners that are not perfectly adapted to the habit, that differ but little from their externally feeding relatives.

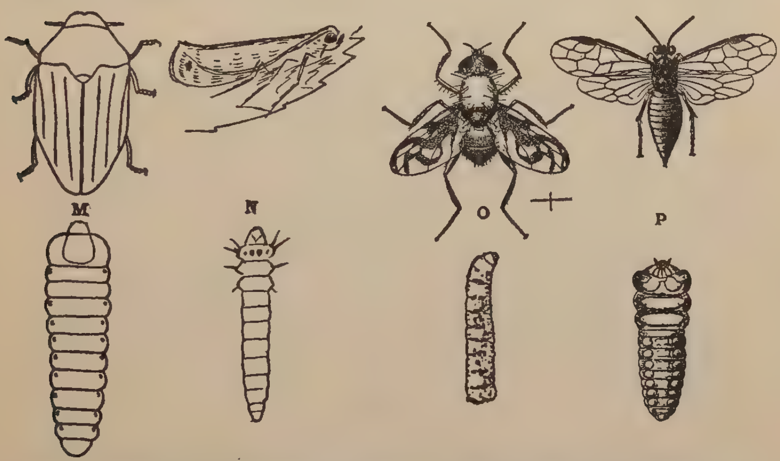


FIG. 4. The four leaf-mining orders and their larva. *M*, a beetle (Coleoptera); *N*, a moth (Lepidoptera); *O*, a fly (Diptera); and *P*, a sawfly (Hymenoptera).

Speaking broadly it may be said that there are but two kinds of larvae found in leaf mines; the Diptera and the others.

The Dipterous larvae are very soft and cylindric maggots, very plastic and of no permanent shape, and able to accommodate themselves to narrow spaces by great changes of form. They readily undergo compression within the shallow mine. They mostly lie on their sides when mining, and hence this pressure is lateral. Freed from compression

the body becomes cylindric, and when fully extended it tapers forward to the mouth hooks. The mouth hooks are swung with an oscillating motion and shear unopposed like a scythe across a swath. The body rolls; and setulae and fleshy protuberances when present are developed in circles and are effective in any position.

The larvae of the other three orders differ from this in almost every particular. The body is flat and of a relatively permanent form. It is generally most flattened on the ventral side—the side next the epidermis of the leaf. It is

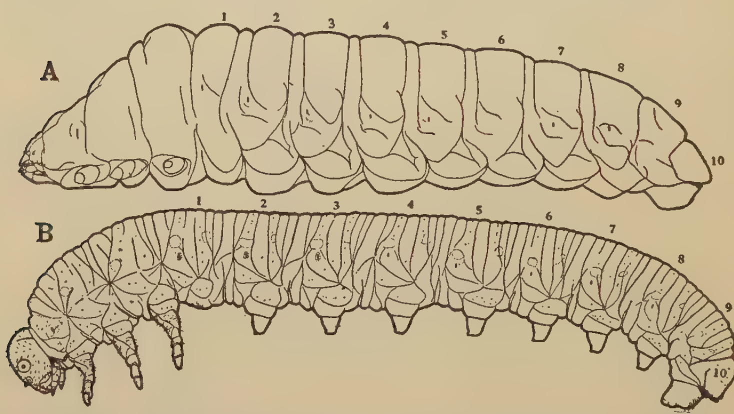


FIG. 5. Two sawfly larvae (after Yuasa). *A*, a leaf-miner, *Metallus rubi*; *B*, an external feeder, *Hylotoma sp.?*

most widened and most strongly chitinized at the anterior end, where flat horny plates both dorsal and ventral cover the prothorax and take the heavy friction against the walls of the mine. Paired jaws are present and they are opposed in action. They work like pincers or shears. The lateral margins of the body become more or less serrate in outline, due to bulging prominences of the middle segments; and ambulatory processes and ambulatory setae are developed in symmetrical bilateral pairs. Details of these adaptations will abundantly appear in the following chapters which treat of the several orders.

In the evolution of a form of body so well adapted to leaf-mining the main tendencies have been toward the loss of legs, loss of color, the flattening down of the body and head, the tapering of the head to a wedge, sloping forward, with the thin mouth parts at its front, the recession of the rear of the head into the wide prothorax with development of strong muscles for moving it forward and backward, in and out, and the development of heavily chitinized dorsal and ventral plates on the prothorax.

LIFE HISTORIES

All leaf-miners hatch from eggs and in the course of their development pass through larval, pupal and adult stages.

The eggs are either deposited upon the surface of a leaf or inserted into it. In the latter case the mother insect makes a puncture to receive it, either by means of her jaws as in the case of certain beetles, or with her ovipositor as in the case of all the sawflies, most of the two-winged flies and a few of the more primitive moths. In Yponomeuta the eggs are laid in masses on the branches of the host and the young worms must wander a considerable distance to find food. The time and place of oviposition vary with the species. The larvae of some of them on hatching from the egg may come out upon the surface of the leaf, but in all the more specialized miners they pass directly into the leaf through the epidermis that the egg covers, and do not appear outside.

The larva is the real leaf-miner. All the work of excavation falls to its share. All increase in size occurs during the larval period. The larva may develop chewing mouthparts capable of devouring cells bodily, or it may develop cell-shearing apparatus and sap-feeding habits. In any case it grows, and passes through a series of larval stages or instars, each of which is terminated by a moult. At the end of each instar it casts off its hard, inflexible, chitinous skin, that has become too close-fitting, and grows a new one.

The number of larval instars, and of corresponding moults varies from three to seven (possibly more in the sawfly larvae), three being the usual number in leaf-mining maggots and beetle grubs, and five in moth larvae. There are sometimes changes of habits with each succeeding moult and these may in some cases be read in the appearance of the completed mine. The Strigifin miner on chestnut (see fig. 40 on p. 123) changes its habit with four out of five of its successive moults.

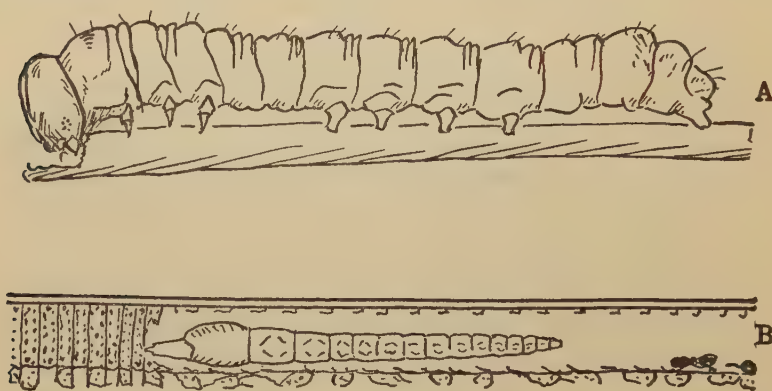


Fig. 6. Two moth larvae. *A*, an ordinary caterpillar that feeds downward; *B*, a leaf-mining caterpillar that feeds forward.

Besides the sudden increase in size that follows upon moulting, there are changes of form that are sometimes very considerable, even before the final change to the pupa. The head capsule is widened with such regular steps that it is possible to read the story of the moultings from a good series of the cast capsules by comparing them as to size. The widths of head capsule will fall into as many groups as there are instars.

The earlier instars are the more plastic, and are more specialized than the later ones. They are more precisely adapted to the operations of leaf-mining. The form in the later instars tends to revert to that of ordinary non-mining

larvae of the several groups. Sometimes there are two distinct forms of larvae and the change from one to the other is so great as to constitute a true hypermetamorphosis. This occurs in the order Lepidoptera and will be discussed and illustrated under that order in Chapter VII (see p. 136). The ordinary larva, as every one knows, has a cylindric worm-like body with a head capping its front end, and mouth parts directed downward. It is, of course, an insect with three main body divisions, head, thorax and abdomen; but the last two are very similar in external appearance, the three rings of the thorax being distinguished from the more numerous rings of the abdomen by the possession of minute jointed legs on each: even this distinction fails when these legs disappear. The ordinary larva feeds downward from the surface to which it clings. The leaf-miner, on the contrary, must feed forward. The ordinary larva creeps freely about, but the leaf-miner is confined within its narrow gallery. To understand the modifications of form that go with the leaf-mining habit we must bear in mind the conditions imposed by the habitat.

The principal needs of the miner in accordance with which all its peculiarities of form have been evolved, are for thin, flat forward-reaching mouth parts, and for holding apparatus to keep them up against the mesophyll for their work. Hence the mouth turns forward, and the head takes on the form of a flat wedge. Walking legs tend to disappear and a variety of stay-apparatus tends to be developed—spacing humps, and tubercles and bristles and bands of setulae, and sometimes an anal sucker. The miners that live in the more solid leaves have the prothorax greatly enlarged, filled with powerful muscles for moving head and jaws, and covered above and below with flat plates of chitin, to take the brunt of the pressure against the walls of the mine. The rear of the head capsule has become more widely opened, and the hind margins have been produced backward within

the prothorax for the attachment of the powerful muscles there. It is the mid-dorsal margin of the head capsule that is prolonged backward in sawfly larvae, the side margins, in mining grubs and caterpillars.

The pupa is, as always, the stage of making over from the worm-like larva into the winged aerial adult insect. It is a quiescent period of variable duration. It is passed in seclusion either in the mine or in some shelter outside, or in the ground. Cocoons are spun by the larvae of weevil miners, sawfly miners, and by most mining caterpillars. Each species has its own way of meeting its own needs.

The adult insects of the four orders are in habits very similar to the other members of their respective groups. On reaching maturity their chief business is mating and egg-laying. The females must seek out proper food plants and deposit eggs in a fit manner to produce another generation.

In the annual cycle there is always one brood per season, and there may be several. The single-brooded forms may be early, requiring soft, young leaves for their operations (see Eriocrania, p. 76), or they may be late in season, waiting until the leaf-tissues are full sized before entering them (see Brachys, p. 190). The repeaters may have a definite number of broods per season, two, three, four, or even more, or the broods may so overlap in time as to be indistinguishable. As with insects of other habits, the number of broods may depend on climate and length of season, there being more of them per year in southern latitudes.

THE MINES

The dwelling places that these small miners excavate for themselves within the leaves differ greatly in details, but they may for convenience be grouped in a few categories.

1. *As to spread* in the leaf, they are of two principal kinds—*linear* and *blotch*.

Linear mines are formed when the larva tunnels straight ahead through the parenchyma. If the course taken be winding they are called *serpentine mines.*

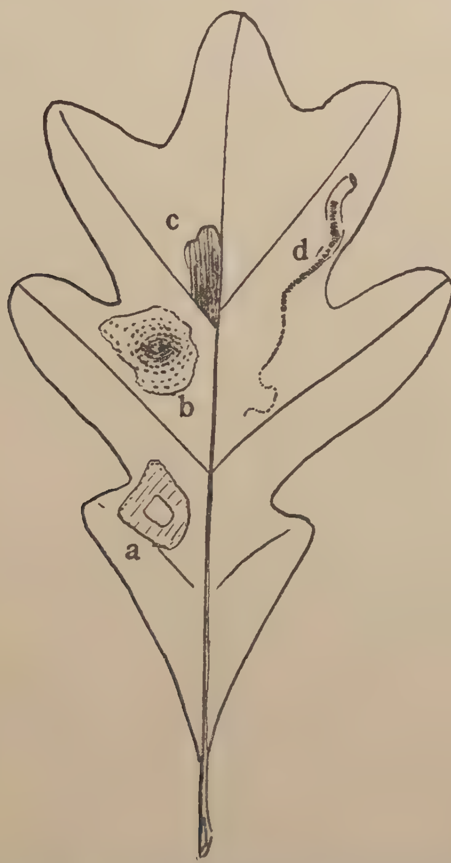


Fig. 7. Mine types. *a* and *b*, upperside blotch mines of Lithocolletis; *c*, full depth blotch mine of Brachys; *d*, a serpentine mine of Nepticula; all on a leaf of white oak.

Blotch mines are formed when the larva excavates a broad patch. The blotch may take on various shapes, circular, oblong, lobed, etc. When a number of slender lobes radiate from its margin, it is called a *digitate mine.*

Between typical linear and blotch mines there are all sorts of intergradations. Often a linear mine expands suddenly and broadly; then it is called *linear-blotch*. Sometimes a mine starts in linear form and widens gradually to flaring margins; then, on account of its outline, it is called a *trumpet mine.*

Many mines start in linear form and become blotched through winding, and intercrossings and cutting out of all the mesophyll between passage ways that were at first separate; but blotches are regularly formed by systematic peripheral excavation, which may be made irregularly or all around or in one general direction only or alternately at opposite ends, or by back and forth "swath cutting" across one end. The boundaries of both linear and blotch mines are generally determined in part by the impeding larger veins of the leaf.

2. *As to depth*, mines may extend from upper to lower epidermis, *full depth mines*, or they may occupy only the uppermost or the lowermost layers of the mesophyll, in which case they are called *upper surface* and *lower surface* mines, respectively. Only the full depth mines are equally visible from both sides of the leaf.

A few linear mines run irregularly through the mesophyll, some of them, while small, appearing first on one surface of the leaf, and then on the other. Most mines become deeper as the size of the larva increases. The terms used in descriptions, unless otherwise stated, apply to completed mines. The very common miners of the genus *Lithocolletis* make a very shallow surface mine during the first three larval instars, completed as to area by that time, and then excavate the remaining mesophyll during the next two larval instars, leaving when completed a full depth mine.

3. *As to finish*, mines may be open or closed. The larvae of moths of the genus *Cosmopteryx*, *Lyonetia* and other genera maintain as an open door a hole in the epidermis

through which they thrust out all their frass, keeping the interior clean and white. Most mines are closed. Those of the Buprestid beetles have the hole through which the larva enters capped with the empty egg shell glued down so securely that it remains in place through the season.

Those unspecialized leaf-mining larvae that wander from leaf to leaf making new mines as they choose, must needs make an opening when they enter; but it is often no more than a slit through the epidermis, and the edges of the slit

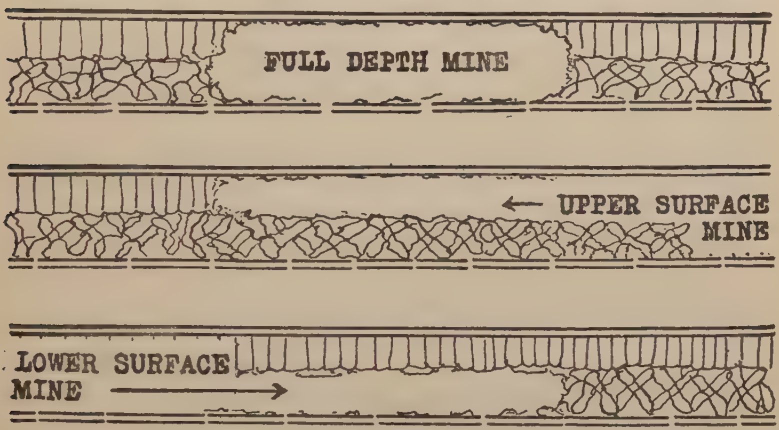


Fig. 8. Diagrams of cross sections of three leaf mines that differ as to depth.

close behind them. The common mode of entrance for all the better leaf-miners is through the attached surface of the egg, leaving no hole for unwelcome bacteria and spores to enter.

4. *As to distribution,* mines often take a definite position or course on the leaf surface, along the margin or along the midrib, originating at the edge and proceeding inward or following between parallel veins (see fig. 11). They may be greatly elaborated, they may take a more or less regular appearance and become star-like or linear mines may curve upon themselves in concentric arcs (see fig. 18). Their

operations may be confined to a small territory or may cover the entire leaf.

Leaf-mining caterpillars spin less silk than do most other moth larvae, but even within the mines silk may serve a variety of uses, such as lining the mine (Tischeria), tying up frass pellets out of the way, and making cocoons. Some highly specialized leaf-miners, notably species of Lithocolletis, increase the space within the mine by spinning silken threads across the loosened epidermis. These threads on drying contract and the mine is thrown into wrinkles or into a single roof-like fold. It is then called a *tentiform* mine. Many details of spinning habits will be found in the chapter on Lepidoptera under the several species, each of which spins in its own way. Mines may further differ in size, in smoothness and color of surface, in transparency, and in manner of frass disposal. This last will often give a clue to the relationships of the larva within the mine. Sap-feeding larvae of the Lepidoptera have little solid matter in their food and hence there is not much frass deposited in their mines, and that little is rarely in the form of distinct pellets. Tissue-feeders, on the contrary, consume quantities of indigestible cellulose cell walls, and reject the cellulose generally in distinct pellets, that are often very considerable in amount and may even seem almost to fill the mine. The manner of bestowal of the frass—whether in central or peripheral midden-heaps or lines, or irregularly, is often characteristic of particular species. It is a very small flat that leaf-miners occupy, and their housekeeping problems are serious. All of the more specialized among them have ways of maintaining free working space and of keeping their food clean.

MINING OPERATIONS

The feeding operations of many leaf-mining larvae may be readily observed with a good lens, holding their leaf up

to the light and watching them at work by looking through the transparent epidermis. However dark colored the body of the mine, the outer margin when freshly excavated is apt to be clear enough to permit the movement of the larvae to be seen. By one means or another—legs, prolegs, ambulatory processes or setae, anal sucker: any or all of these—the body is held rigid while the jaws are moved up against fresh mesophyll. But there is a great difference in jaws and consequently in manner of attacking the mesophyll. If one watch the larva of a beetle like Zeugophora or of a sawfly like Fenusa, the head will be seen to be thrust forward and drawn backward, in and out of the prothorax at every bite. The opened mandibles are driven forward into the new tissue, closed and withdrawn with each movement of the whole head forward and backward. The prolongations of the chitinous shell of the head to rearward have muscles attached that control this in and out movement.

If one watch a highly specialized sap-feeding Lepidopterous larva in its mine the thin, flat, saw-edged, wall-shearing mandibles will be seen to be moved steadily along, oscillating as they go, cutting a thin slit through one cell-layer only, while the freed cell contents as steadily flow into the mouth of the caterpillar. Generally in these mandibulate larvae the ventral side of the body lies flat against the epidermis.

In contrast with this, the Dipterous maggot lies on its side in the mine, as already stated, and swings its mouth hooks vertically; i.e., in the median plane of its body, parallel to the leaf surface. The body remains stationary except at the anterior end, which swings in the arc of a circle as the shearing of the mouth hooks proceeds. On certain plants, like the windflower, *Anemone pennsylvanica*, the shorn cellulose walls lie in the mine in swaths, like leaning stubble cut with a dull scythe, and show exactly the course the larva has taken from side to side within the interspaces that are bounded by the stronger veins. The

larva cuts the swath across the end of the blotch mine, doing all its cutting in one direction, scythe-like, across the field, and at the end of its reach swings back idly to the

FIG. 9. Diagrams of the mines and mining operations of a Dipterous leaf-miner on Anemone. *A*, a leaf with three mines; *B*, a portion of a mine enlarged; *C*, a smaller portion of the same, more enlarged; *D*, the "swing" of the larva as it cuts successive "swaths."

starting point, hitches up closer, and makes another cut. And when the swath has reached the edge of the vein-bordered field that is being harvested, the larva rolls over

(thus reversing his sickle), turns about and cuts another swath back across the same field. The cross strokes of the swath are always concave to rearward, as swinging in an arc, necessitates. It follows that going and return swaths have opposed concavities. A rather beautiful herringbone pattern results from this, made in a single line of progression, back and forth, redoubled, wavering at vein barriers and becoming regular again when new leaf areas are entered but continuous from the beginning to the end of the mine; and in it one may read the complete record of the miner's travels.

FIG. 10. A leaf of ragweed, collapsed where mined by the moth, *Tischeria ambrosifoliella*.

The effect of the mining-operations on the plant varies with the character of the leaf, as well as with the extent and nature of the injury to the tissues. Thus the firm leaves of the oaks stand up well under the attacks of a great variety of miners, while the soft leaves of garden herbs, often collapse rather quickly after even moderate injury. The structural strength of the parts surrounding the mine determines this as is well seen by comparing the mines of two species of Lithocollitis,—belonging to the group that, in the late larval instars, normally makes tentiform mines. The

mine of *L. lucetiella* is located on the underside of a linden leaf between strong veins, and it remains quite flat to the end. But the mine of *L. morissella* on the underside of the thin and weakly braced leaf of the hog-peanut, becomes completely folded together in a single ridge: collapsed-tentiform, so to speak. (See fig. 41.)

Certain portions of the leaf are preferred by different leaf-miners, some, like Brachys, choosing the vicinity of

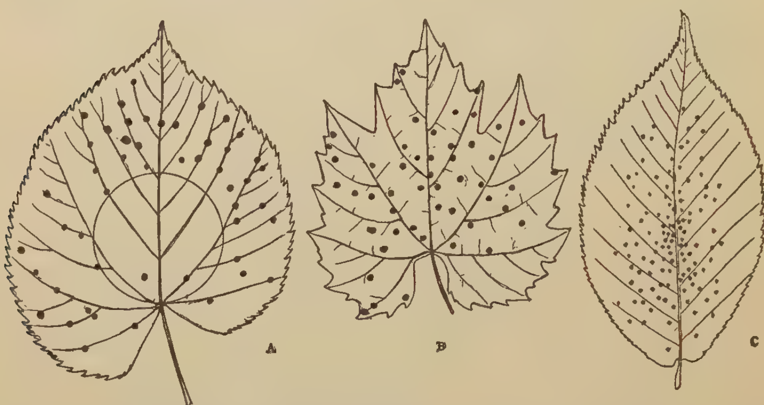


Fig. 11. Leaf-maps of mine distribution. *A*, 50 mines of *Brachs* sp.? on Basswood (note their scarcity within the central circle); *B*, 50 mines of *Antispila viticordifoliella* on wild grape (general); *C*, 100 mines of *Lithocolletis ostryarella* on hop hornbean (note avoidance of the leaf margin).

the stronger veins, and others avoiding these as much as possible.

FRASS

As an African hunter follows his big game by taking note of its spoor, and as an ornithologist learns something of the habits of owls from the examination of their pellets, so the student of leaf-mining insects may gather much information concerning their identity and their behavior from an examination of their frass.[2] This varies with their food,

[2] Frass is the rejectamenta of their food (as the name implies) left in the mine after feeding, and of their feeding operations: fecula, chips, etc., collectively.

according to the nature of the leaves in which they mine, and with their size, in amount, color, consistency and disposition.

A few leaf-miners eject all their frass through a hole in the epidermis of the leaf. The dainty little herb-mining larvae of the genus Cosmopteryx thus keep their mines clean and white. At the opposite extreme are some of the cylindric Lepidopterous larvae and the sawflies, whose mines are almost filled with frass pellets; also some of the Dipterous larvae whose smeared-up mine-walls have a very messy appearance.

The arrangement of the frass in the mines of certain species is very characteristic. In the mine of the maggot of *Phytomyza nigritella* on peach and cherry the frass is arranged in a distinct line of spots, that is at once distinctive. So, also is the crossbanded arrangement of it in the winding part of the mine of the trumpet miner of the apple (see figs. 2 and 3 of pl. 2).

The digitate leaf-miner of the locust, *Parecopta robiniella* maintains a sort of storage cellar for frass down next the lower epidermis of the leaf, while it lives and mines in the palisade layer of cells close to the upper epidermis. It is said to dump its moulted skins, like castoff clothes, into the same receptacle. The makers of linear mines, as they move forward, leave their frass behind in continuous or broken, straight or zig-zag lines or in spots. The polygon miner of the basswood, *Lithocolletis luciella*, bestows its frass pellets in the extreme periphery of the mine while it feeds from the outside toward the center. Many other mining caterpillars store it in the center, or in one end, often webbing it in place with silk. Most of them keep their feeding areas clear of it.

TENANCY

The time during which a leaf mine is occupied may vary from less than a single larval instar to the entire develop-

mental life of the insect. Here again, permanence of residence within a single mine is a sign of better adaptation to the leaf-mining life.

Some of the less specialized leaf maggots seem to slip in and out of a soft leaf at will. Encountering a vein, they cut a slit in the epidermis and slip out through it; and, presently in a new place, cut another slit and slip into the leaf again. The locust leaf-mining beetle, *Chalepus dorsalis*, regularly occupies several leaflets in succession; when it has finished the mesophyll in one leaflet it rambles off in search of another one. The grass leaf-miner, *Aphelosetia orestella*, occupies one leaf of bottle-brush grass, *Hystrix patula*, in the late season and hibernates in it; but this old leaf is frozen in the winter, and in the spring the larva enters a new leaf and completes its growth there. Others of this genus have similar habits.

This subject will receive special treatment in our discussion of the order Lepidoptera, in which order all the grades of tenancy are best illustrated; but here it may be said that most leaf-mining larvae spend their entire larval life within a single mine, and many pupate there, either with or without a cocoon, and either attached to the wall or free. More often the pupa is formed outside, in a crevice or a fold of the leaf or in the ground.

THE ORIGIN OF THE LEAF-MINING HABIT

It is probable that the leaf-mining habit has been acquired independently many times. The Buprestid beetles may well have come to it through their wood-boring habit. Many of them live in succulent twigs and originally they may have come into the leaf blade by way of the stalk. At any rate, their earlier stages are more typically of the form of body of the wood borers and the later stages are more cylindric. The mines are often started upon the surface of a vein.

Dipterous larvae, accustomed to burrowing in soft substances, may have come to the mining of green leaves through the habit of boring in dead ones. At any rate, there are species that still do both these things and that are sometimes saprophytes, at other times leaf-miners, being not wholly committed to either habit.

But it seems probable that leaf-mining caterpillars and sawfly larvae and leaf-beetle grubs are derived from forebears that fed on leaves in the ordinary way. Perhaps the earliest among them merely ate a hole in the leaf: later ones put their heads farther in and kept on eating down underneath the epidermis: finally some of them bodily followed their heads down into the hole and dwelt there.

INTERGRADATION WITH OTHER HABITS

Leaf-mining as a mode of life intergrades with gall-making, with stem-boring and with feeding from shelter. All these shifts for a living are common enough in the insect world. Each has its host of strict adherents, but there are borderline forms that combine two or more of these ways of getting on.

Gall-making insects enter the leaf while its tissues are still in a formative state, and stimulate it to overgrowth and to remarkable secretory activity. They do not need to mine the tissues, for they possess the power to stimulate the plant to produce both food and shelter. From the walls of the gall chamber they lap up the food that the tissues prepare for them and bring to them. This is a wonderful power, but not all gall-making insects possess it to the degree that is sufficient to meet all the needs of their larval life. A number of them that are true gall-makers at first, have to resort to the use of their jaws in ordinary foraging when of a larger growth. The tulip-tree blister-gall maker, *Thecodiplosis liriodendri*, for example, at first makes a thick-walled discoid gall within the leaf, and later eats most of it

away before completing its growth. The little caterpillar, *Heliozela aesella,* does likewise, in the leaves of grape. By the time it has finished its tenancy the walls of the gall are almost wholly consumed. The sawfly larva that makes the familiar "apple galls" on the leaves of willows when full grown and of larger appetite has to resort to the ordinary use of its jaws, as is evidenced by the large, irregular, frass-filled cavity[3] that it then excavates.

FIG. 12. Leaf of tulip tree, bearing six mined-out gall of the midge *Thecodiplosis liriodendri.*

Stem-boring and bast-mining and leaf-mining are habits closely akin. Stem-boring probably came first since the

[3] The case of the leaf-mining fly of the iris *Agromyza laterella* as detailed by Claassen (1918) is quite different, and quite unique. This larva is a true leaf-miner. When grown it bores down into the undeveloped iris bud to form a pupation chamber. The presence of the pupa there when growth starts in the spring, causes a gall to develop; but its development is quite incidental: it profits the fly nothing.

greater thickness of stems requires less alteration of the ordinary larval form.

FIG. 13. A leaf-tyer of Southern California that is also a leaf-miner (undetermined). *A*, a spray of *Baccharis viminea*, bearing a leaf-tie; *B*, a single leaf detached, its upper portion mined above the entrance hole; *C*, the silken bag containing the larva, removed from the center of the tie.

The surface of a stem when it is green and covered by a smooth and transparent epidermis, is not very different from that of a leaf. Some observations made by one of us

(Mrs. Tothill) in Vancouver on the madrona leaf-miner, *Marmara arbutiella*, indicate how easy is the passage from stem to leaves. In some cases the mining of a single larva is confined to a single leaf; in some cases the larva does not enter a leaf at all but tunnels up and down under the cuticle of the shoot. In many cases, however, the mines either begin in the leaves and pass by way of the leaf petioles down under the epidermis of the shoots, or, beginning under the epidermis of the shoots pass up the petioles into the leaves. In a few cases the mine begins in one leaf and passes by way of the petiole into the shoot and then up another petiole into another leaf. The surface of green apples is sometimes mined by another species of *Marmara* (*M. pomonella*, (fig. 4, pl. 2); and the phyllodia of prickly pears (species of Opuntia), by the larger larvae of the Phaloniid moth, *Melitara prodenialis*. In the chapter on Lepidoptera a number of examples will be cited[4] of moth larvae that mine the blade of the leaf while very small, and the strong veins and stalk when older and larger. The natural cavities of some leaves provide a home for certain unspecialized young larvae of Noctuidae.[5] These cavities are soon outgrown.

Feeding from shelter is often combined with leaf-mining, and in a variety of ways. A leaf-tyer of the southwestern United States, when it has fastened together with silk three or four leaves at the summit of the wandlike stem of *Baccharis viminea* and has spun about itself a white silken bag in which to dwell, makes a hole in the upper end of the bag, where it is attached to a leaf, and eats through the epidermis of the leaf and then mines the leaf through this hole. It lives well up in the bag and deposits all its frass in a midden heap at the bottom. It reaches out of the holes at the top (one into each leaf that it mines) and feeds there without

[4] See *Phthorimaea operculella*, p. 159; *Acrocercops strigifinitella*, p. 124.
[5] See *Arzama obliqua*, p. 176.

exposing itself. All the feeding is done from the holes upward, and full depth blotch mines are formed.[6]

The only alteration of such a habit that would be necessary to make a confirmed leaf-miner would be the abandonment of the bag.

The leaf-sewer of the hog-peanut, *Stilbosis tesquella*, manages the matter a little differently. It draws one

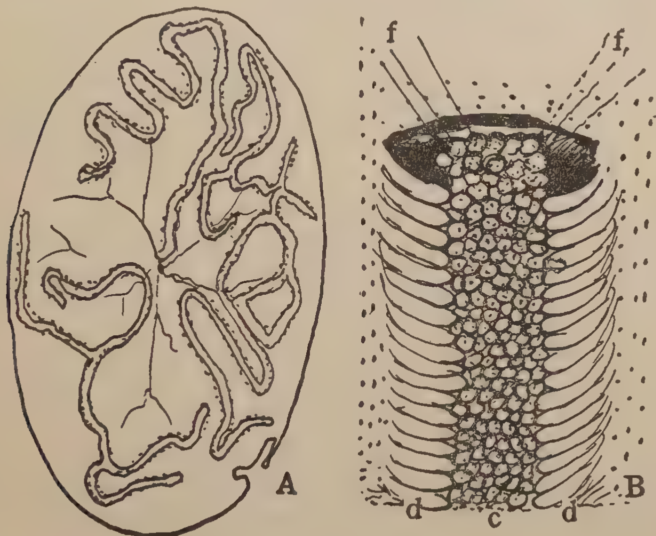


FIG. 14. Diagrams of the mining operations of the midge *Chironomus braseniae*. (After Leathers.) *A*, a leaf of watershield showing the tortuous mines in the upper surface; *B*, a bit from the forward end of one of these mines showing at *c* the pellets of frass held together with silk, that form the roof of the mine, lying between the elevated side strips *d*, of partially dissevered epidermis, and extending forward in a sort of porch upheld by a few silken stay lines, *f*.

leaflet flat upon another and sews the two together with stitches of white silk placed about an eighth of an inch apart all about the edges where in contact. For further security it adds a few central stitches joining the stronger veins.

[6] See further in this connection the accounts of *Recurvaria piceaella*, p. 165, and *Argyresthia annetella*, p. 171.

Thereafter it feeds within the narrow space quite as do its leaf-mining relatives; it lies on its flattened back and feeds from the leaflet on the upper side, clearing away the mesophyll and leaving only the upper epidermis. (See fig. 41.)

Conversely, the locust leaf-sewer, *Gelechia pseudoacaciella*, is said to invade the mines of other little moth larvae when young, later betaking itself to a home of its own between two leaflets sewed together.

There is a little greenish-yellow midge, *Chironomus braseniae*, whose larva is a sort of leaf-miner. It trenches the upper surface of the floating leaves of the watershield, *Brasenia schreberi*, roofing over the trench with loosened epidermis and with frass, and it lives and feeds within the trench as in a mine. Apparently it does this only when well grown; for the trenches are all of about one diameter: they do not increase as do true linear mines with growth. Its earlier larval habits are still unknown.

Its method differs from true leaf-mining chiefly in that it cuts the epidermis as it goes. From the middle line of the trench it cuts this in narrow strips extending to the side margin, then it removes the thick palisade cells from beneath them. Then it elevates them at their free inner ends, like the strips of a slat roof, fills in the middle interspace with loose pellets of frass and binds all together with silk. Thus its trench is completely covered. At the end it makes a slight enlargement for a pupation chamber. When the adult midge emerges the empty pupal skin is left partly protruding. Many interesting details are given in Leathers' (1922) account of its work.

There are in our Southern States little caterpillars of the genus Homaledra, that make covered trenches in the leaves of palmettos and excavate parenchyma from their trenches. There is one species for each surface of the leaf; *H. sabalella* chooses the upper surface and lives gregariously in irregular runways that are sheltered under a roof of brownish frass

pellets, webbed together with silk, and looking like old weather-stained sawdust. The other species, *H. heptathalama*, lives solitarily in a fold on the underside of the leaf, and makes for itself a frass-roofed, linear, seven-roomed house, of altogether unique character. From Busck's brief account of it we quote the following description:

> It begins by making a small, elongate chamber and adds, as it grows, successively larger, more or less rectangular, thick-walled, communicating rooms to its house, the entire length of which is 1½ to 2 inches, and which when finished contains 7 (or sometimes 8) chambers; hence the name of the insect.
>
> It pupates inside its case, and the moth issues through a round

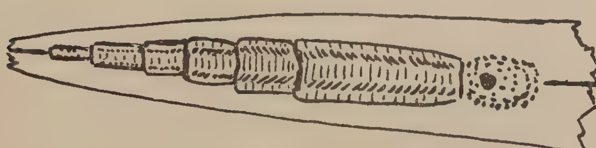


FIG. 15. The seven-chambered house (roofed-in mine) of *Homaledra heptathalama* on palmetto. (After Busck.)

> hole in the last chamber. This is different from the other chambers, being rather loosely built. The other chambers are very firm, smoothly finished outside, dark brown. The pupa is brown, very slender, antennae and wing-cases reaching only halfway down the abdomen. Pupa skin is not protruded at issue.

The genus Homaledra includes the two species of aberrant habits mentioned on page 28. Both occur on the palmetto. Both mine from shelter, but the one on the lower side of the leaf, *H. heptathalama*, is solitary, and the one on the upper side, *H. sabalella*, is gregarious.

ENEMIES

Like other animals, leaf-miners have both predacious and parasitic enemies, and as yet comparatively little is known

about either. They are too small to be very attractive to the larger and more familiar animals, and too small to be readily observed by us when sought out and eaten, as doubtless they are, by warblers, creepers and nuthatches. Forbush says that the beet leaf-miner is eaten by chipping sparrows. At Picton, Nova Scotia in 1908 there was a heavy infestation of birch leaves by sawfly that over winter in a circular silken hibernaculum within the leaves. Dr. Matheson found most of the hibernacula empty, with a small hole in one side, wherein, presumably, some bird had extracted the larvae. Many larvae are taken from their winter quarters by mice and shrews. When one sees a little red squirrel sitting among the fallen leaves under a red oak tree, tossing a handful of leaves and cocking his head on one side as if intently listening, it is easy to imagine that he is trying to catch the sound of a loose pupa of the beetle Brachys, tumbling about within its mine. Dr. Martin Hering in his comprehensive work on "the Ecology of leaf-mining Insects," mentions inquilines and symbiotic dwellers namely; thrips, fungi, yeasts and bacteria, in the mines of these insects.

Predaceous insects are rather more commonly observed. Webster and Parks (1913) record a species of mite (*Erythraeus sp.?*) attacking the larvae, of *Agromyza pusilla* within the mines. One of us (Frost) has seen the bug, *Nabis ferus* feeding on larvae of *Pegomyia calyptrata*, and *Chrysopa rufilabris* feeding on *Agromyza jucunda*. The Nabis has also been reported as an enemy of the beet leaf-miner. More is known concerning parasites because every one who tries to rear leaf-miners finds emerging in his cages plenty of these instead. In the beginning, the mine may have been a place of comparative security from parasites, but it is not so now. Once the parasites has learned how to effect an entrance, the miner is worse off than its free-living ancestor, having no means of escape. A very high percentage of parasitism is the rule among leaf-miners.

There is no existing list of the known parasites of leaf-miners, but one of us (Frost, '24: 131–132) has compiled a list of those known from Dipterous miners. This list of 67 species includes at least one secondary parasite.

COLLECTING AND REARING LEAF-MINERS

It is easy to collect leaf-mining larvae. All that is necessary is to gather the leaves and hull the insects out from their mines. A fine, curved-pointed pair of forceps is the most useful instrument for this, though a hook-pointed needle in a handle will do it almost as well. The larvae are best preserved in alcohol of about 80 per cent strength. Very soft larvae, like those of the Diptera, are better preserved if first dropped for a minute in boiling water, before being put in the alcohol. Pupae that are formed in the mines, are obtained and preserved in like manner. But it is very difficult to find pupae in nature when formed outside the mines, and they are better obtained by rearing them.

The best way to rear leaf-miners when they are common and near at hand is to let them rear themselves as far as possible: to keep watch on their progress and to gather the material when in the desired condition. The one rule for success in rearing any thing is to *maintain natural conditions*. Since this is rather hard to do in parched leaves, it is better to leave them on the stems whenever it is possible to watch them there until the larvae are full fed. Then they may be put in containers provided with proper conditions for formation of pupal cells—earth, trash, leaves or rough twigs in the bottom, according to the demands of the species; or if they pupate in the mines, then nothing at all besides the leaves containing them.

The adult moths, beetles, *etc.*, when they emerge are pinned and mounted by the methods well known to every entomologist.

Method of collecting Dipterous leaf-mines. For collecting

Diptera, a round, seamless, tin box is used, a separate box for each host plant and for each of the different types of mine found on the same host plant. The proper records are placed in the respective boxes. As a rule, the leaves remain fresh in the boxes until the larvae have transformed. This method requires a large number of boxes, and there is a limit to the number that one can conveniently carry. There is a more compact method. The leaves containing the miners may be folded in tissue-paper triangles, much as many entomologists use for duplicate material. These small packages are then placed in a tin box. The box retains enough moisture to prevent the leaves from drying out, and leaves from many different plants may be placed in the same box without confusing the records. If the larvae transform before reaching the laboratory the puparium will be found within the envelope with their records.

Ordinarily the larvae are not yet mature when they reach the laboratory, and it is therefore necessary to allow them to continue to feed. Larvae that naturally leave the wilted leaves and enter the fresh ones are easy to rear, but those that do not go to the fresh leaves are more difficult. Often the leaves wither or decay before the larvae are full-grown.

When the larvae transform they may be removed to small vials by means of a camel's-hair brush. The vials are then closed with cork stoppers in order to prevent evaporation during the short period of pupation. When a larva transforms within the leaf, the puparium is cut from the leaf and allowed to dry for a few hours before the cork stopper is placed in the vial. The puparia are kept in these vials until the adults emerge. The adults should be kept alive for several days in order that they may attain their proper color, since teneral specimens are practically indeterminable, especially among the Agromyzidae. Leaves bearing mines may be preserved as herbarium specimens, mounted on white cards, with the name of the family, the genus, and

the species, of both the host plant and the insect mining the leaf. A thin sheet of celluloid may be placed over each of the mounts. Most of the herbarium specimens show very clearly the arrangement of the frass within the mines, the exit holes of the larvae, and other characters of interest. Photographs have the advantage of being more durable than the herbarium records, but they are far from being as accurate and as rich in minute details.

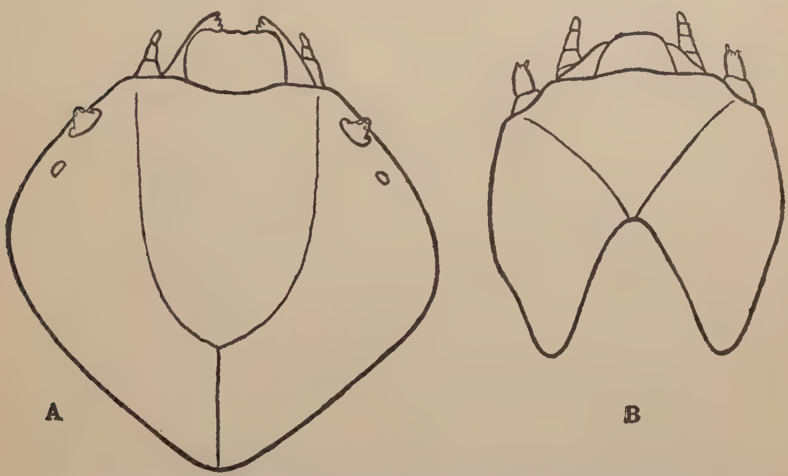


FIG. 16. Diagram illustrating head form in two orders of leaf-mining larvae. *A*, a sawfly larva (Hymenoptera); *B*, a beetle larva (Coleoptera).

How to identify leaf-miners. First collect them, and get the name of the plant on which you find them. Then look in the list on page 302 to see what insects are known as miners in the leaves of that species of plant and of others near akin to it; that is, in members of the same plant family. Among these you may find your specimens described; so note carefully the form and depth and spread of the mine, the presence and distribution or absence of holes, silk and frass, and the form and structure of the larva within it. The table on page 35 may then be used to determine the

order to which the larva belongs, and among the members of this order that infest the leaves of this plant you may find your leaf-miner described. For final certainty of determination it is always best to rear some adults from the larvae and have them named by a specialist in the group to which they belong.

TABLE FOR SEPARATING THE LARVAE OF LEAF-MINING INSECTS*

ORDER	HEAD-CAPSULE	OCELLI	MOUTH PARTS	STEM OF EPICRANIAL SUTURE	OCCIPITAL REGION	BODY FORM	THORACIC LEGS	PROLEGS	POSITION OF THORACIC SPIRACLE
Lepidoptera	Present	1–6 pairs†	Mandibulate	Present or absent	Concave	Depressed	Present or absent	Present or absent	On prothorax
Coleoptera	Present	Absent or reduced	Mandibulate	Absent	Concave‡	Depressed	Present or absent	Absent	On mesothorax
Hymenoptera	Present	1 prominent pair	Mandibulate	Prominent	Convex	Depressed	Present or absent	Rudimentary	On prothorax
Diptera	Absent§	Absent or reduced	Mouth hooks	Absent	When present incomplete	Cylindrical, tapering	Absent	Absent	On prothorax

* Modified from Frost, 1925, p. 405.

† Rarely one ocellus.

‡ Except in Buprestidae in which case the pro-thorax is greatly enlarged and the head is retracted.

§ Head-capsule present but incomplete in the primitive Diptera (Tipulidae, Chironomidae and Cecidomyiidae.)

CHAPTER II

Extent of the Leaf-Mining Habit

ECONOMIC SPECIES

It is a matter of no little biological interest that the most highly specialized and most numerous leaf-miners do little harm to the plants whose leaves they inhabit. In such great genera as Nepticula and Lithocolletis there are no important economic species. These enter the leaf and feed within it in such a way as to cause a minimum of disturbance or of damage. These have found a way of living that lets the leaf live also. These represent the acme of ecological specialization. Their business is on a permanent basis. They live in the same localities in the same plants in about the same numbers year after year.

One of these flat, legless, crossbanded, specialized larvae with cell-shearing, sap-feeding mouth parts, *Lithocolletis guttifinitella,* lives on poison ivy. It makes broad, tortuous, whitish, upper surface mines, that take on shapes as varied as those of water spilled on a smooth surface. These seem to be spread over almost every leaflet in many ivy patches in early autumn; yet the plants appear to be thriving. Several larvae are at work together in nearly every mine. When one sees how very abundant they can be in this noxious plant, it seems almost a pity that their methods of feeding injure that plant so little.

The injurious species of leaf-miners are less specialized and less steady going. They eat more of the leaf substance, and they damage more than they eat. They disfigure their host plants leaving them draped in seared, shrivelled, tattered foliage. They are part-time leaf-miners, like the

tobacco split-worm (*Phthorimaea operculella*) that is now in the leaves and then in potato tubers in storage, or like the lilac leaf-roller that mines the leaf while small, and then rolls it up from the margin and lives and feeds thereafter in the roll; or like the ribbed cocoon-maker of the apple (*Bucculatrix pomifoliella*) that mines during its first instar only, and thereafter feeds openly upon the leaf. Or, they are general feeders like the beet leaf-miner, *Pegomyia hyoscyami*, now here, now there, accepting whichever food plant offers, only confining themselves to a group of related plants.

Leaf-miners infest many of our cultivated crops, but few of them are of economic importance. The apple has at least ten different North American species that mine its leaves (see Chapter XVI, p. 313); two or three of them are of some importance, occasionally, in ill-kept orchards. Newly imported leaf-miners that are running ahead of their parasites are apt to be most injurious—until their parasites catch up with them. The Fenusa miner on birch, the Schizocerus miner on European alder, and the Gracilaria miner on lilac are examples of recent immigrants into the Eastern United States, that now (1925) are causing unsightly foliage wherever they occur. The so-called "wheat leaf-miner," *Alphelosetia praematurella*, a native species, is only a scatterling in the leaves of wheat, its preferred food plant being wild rye (Elymus).

The most important economic species are probably those affecting vegetable crops, such as the beet leaf-miner, *Pegomyia hyoscyami*, the tobacco split-worm *Phthorimaea operculella*, and other species affecting cabbage seedlings, celery and peppers. The chrysanthemum miner, *Phytomyza chrysanthemi* is a real pest in the greenhouses of the commercial floriculturist. The coffee leaf-miner, *Leucoptera coffeella*, is a serious hindrance to the growing of that crop in Porto Rico, since its great blotch mines reduce the working

capacity of the leaves. Our maple sugar crop is considerably reduced each year by the operations of the little leaf-mining casebearer, *Paraclemsia acerifoliella* (see p. 78). Very unsightly foliage effects are produced by a good many leaf-miners on trees, notably by *Gracilaria syringella* on lilac, by *Chalepus dorsalis* on locust (Chittenden, Hutchings, 1924), by *Zeugophora scutellaris* on poplars, and by several imported sawfly miners on elm, alders and birches; also, in coniferous trees by *Argyresthria thuiella*, in arborvitae (Britton, 1922) by *Recurvaria piceaella* on spruce (Gillette, 1922) and by *Coleophora laricella* on tamaracks (Herrick, 1912). There is hardly a meeting of economic entomologists held anywhere but that receives reports of injurious abundance of leaf-miners in field, garden or orchard crops.

Control methods for leaf-mining insects are only beginning to be well worked out. Arsenical poisons are, of course, unavailing (unless to adults) since they cannot be applied to the food of the larvae, covered as it is completely by the epidermis of the leaf; but good results are obtained by the use of rather strong outdoor applications of nicotine sulfate, oils, and other contact insecticides; also by fumigants, when the plants may be inclosed for treatment, as in a green house.

HOST PLANTS

Our list of plants, in Chapter XVI will give specific information as to where leaf-miners have been found. It is a long list and it includes nearly all the more familiar seed plants. These range in character from succulent purslanes and thin grasses to stately trees. In general it may be said that leaf-miners prefer the better constructed, and longer enduring leaves of woody plants.

The groups of plants sought by the most species are the *Amentiferae*, especially the willows, poplars, birches and oaks (the oaks before all) and the rose family. The maples, legumes and composites have a fair proportion. A few are

found on ferns. Excepting attacks by the Diptera, herbs have in general fewer leaf-miners than have shrubs and trees.

Sometimes a genus, or the species of a natural division of a genus, will show a preference for closely related plants. Thus the caterpillars of the genus Aphelosetia all mine the leaves of grasses and sedges, and those of Mompha and Laverna show a marked preference for members of the evening primrose family, especially for Oenothera and

FIG. 17. A leaf of walking-fern (Camptosorus) bearing two mines, one with a fixed puparium protruding.

Epilobium. The beetle grubs of the genus Phyllotreta mine the leaves of crucifers. The food plants of some one hundred and eighty species of Lithocolletis are known. Nearly all of these are found on trees and shrubs of the amentiferous groups, *forty-four* being attached to the genus of oaks (Quercus) alone.

The plants attacked by any one species of miner usually are of one species or of a group of nearly related species.

Hence there is no better clue to follow in identifying leaf-miners than the name of the plant in whose leaves they are found.

Some of them live in plants that are to us poisonous or otherwise offensive, but their dwelling place is the soft, nourishing parenchyma well apart from noxious products. The aromatics of the mints and the irritants of the poison ivy are produced in epidermal hairs, far over their heads, and the latex of milkweed is in special vessels in the veins beneath their feet. However, if we open a number of mines of the little fly, *Agromyza pusilla,* in milkweed leaves, we are likely to find that now and then some careless maggot has cut into a latex vessel, and it has leaked into the mine and formed a white clot there; and occasionally we may find a larva dead and buried in a large clot, having paid the penalty for his careless operations.

CHAPTER III

Order Lepidoptera

This is the order in which the leaf-mining habit has been best developed. Here it attains the polish and precision of an ancient and perfected art. Lepidopterous leaf-miners are the most abundant and most interesting of all.

Fig. 18. Mine of Chrysopora on Chenopodium

Lepidopterous leaf-miners were known of old. The great naturalists of the sixteenth century who first made careful and authentic gatherings of insect lore, filled many pages of

their works with sprightly accounts of the ways of these little creatures. Men like De Geer and Raeumur found them full of interest. To catch the spirit of these old-time naturalists one cannot do better than to read De Geer's account[1] of a "yellow mining larva which makes galleries in the leaves of the rose." This leaf-miner was first discovered by De Geer in 1737. Many years afterward, when binomial names become current, Goeze gave it the scientific name *Nepticula anomalella*. De Geer's account is quaint and painstaking. Let the flavor of the times and of De Geer's personality justify the rambling length of it. It would seem to be the first time that an inquiring eye had ever lighted on an Nepticulid larva. It is certainly the first account of the rearing of one.

In autumn, in the months of September and October, we find on the roses (whether wild or growing in the gardens) leaves which are marked with brown streaks which are wavy and, as it were, entwined in one another. If we examine these streaks we soon perceive that they are the work of insects, that they are channels mined by tiny insects in the interior of the leaves. If one holds them towards the light one may see distinctly the mining insect at the larger end of the channel.

The insects which make these passage-ways are particularly noteworthy on account of their very unusual form which departs widely from that of all their kind at present known. They are true caterpillars, but caterpillars of an altogether new and special sort. They are very small, their length is at most but two lines (4 mm.). They are of a beautiful yellow color bordering on orange but the head is brown. The body is divided into twelve segments and tapers posteriorly. . . . . The transparency of the skin allows one to see some of the internal structures. . . . . The head is supplied with two, flat, slender teeth well adapted for

[1] Translation by Mrs. Tothill from De Geer's *Memoires*, Vol. 1, p. 446, *et. seq.*

gnawing and loosening the pulp of the leaf without injuring the upper membrane; if they were larger the caterpillar could not

FIG. 19. A copy of DeGeer's figures of two leaf-miners (Nepticula and Lithocolletis) prepared nearly two hundred years ago.

work them so dextrously in so thin a leaf. These teeth project considerably in front of the head. . . . . Below the head is a

spinneret having the form of a small, elongate nipple considerably like those of ordinary caterpillars. This spinneret is difficult to see but nevertheless I saw it quite plainly with a long thread that the caterpillar had just spun still attached. . . . .

In order to see the very remarkable legs it is necessary to look at the caterpillar from the side with the help of a strong lens. They are eighteen in number and placed all along the under side of the body in two rows. They are very like the membranous legs of saw-fly larvae; their shape is pyramidal or conical, and they are entirely without hooks. They differ from the legs of other caterpillars even in their arrangement on the insect's body; for they are placed on the nine consecutive segments which follow immediately after the first, and each of the nine segments has a pair of them. It is, then, the first, the eleventh and the twelfth or last segments which lack legs.

I looked at these caterpillars many times, and I looked at many of them in order to make myself sure of the number and appearance of their legs. That was in the year 1737. But I was not satisfied even with that; nine years afterward, in 1746, I repeated my observations, I examined afresh the legs of the caterpillars of this species and again I found them exactly as just described. One cannot sufficiently verify new and singular observations.

These caterpillars mine as we have said, in the interior of leaves where they make a sort of tunnel. One may find leaves with three different tunnels, mined by three caterpillars; but ordinarily each leaf is inhabited by one. The transparency of the upper membrane makes it possible to see the insect through it.

To see whether the leaves are mined one must look at them from above, for the insect mines them in such a way that on that side there remains only the membrane; the lower side retains a part of the fleshy substance, the caterpillars consuming but half the thickness of the pulp within the leaf. But by holding the leaf up to the light one can see equally from either side whether it is inhabited. With the help of a lens one may also see in this way how the caterpillar mines the leaf. One may see how with the two teeth that it has in its mouth it bites into the fleshy substance, how it loosens, piece after piece in succession, tiny bits that it immediately swallows.

The tunnels do not go in straight lines but bend in very irregular curves; as the caterpillar mines now on this side and now on that, it often crosses the tunnel already made. . . . . Except for that one could easily tell the beginning of the tunnel or the place where larva began to mine. . . . . At the beginning the place where the caterpillar commenced to mine, the tunnel is no bigger than a hair but it goes on getting bigger all the way to the end, where it is largest.

These paths dug out in the leaf have a dull brown color from their beginning for about half their length. This color is due to the excrement which is enclosed there, taking up the whole mine. But the other half, or rather more, is not entirely filled with excrement; only all along the middle is seen a line or continuous streak of brown excreta. The empty shells on either side appear whitish because that is the color of the epidermis of the leaf. I have noticed a rather curious thing about the excrement of these little insects. In the first two quarters of the mine's length the masses are perfectly continuous. Together they make up a single body in the form of a thread which occupies the whole space of the tunnel as we have just said. They have the appearance, then, of having been liquid. The third quarter of the gallery is taken up by excreta that hold together also, but which occupy only the central part of the tunnel's width. A curious thing is that this thread goes zigzaging in curves from one side to the other. In the last quarter of the mine one may see that the excreta are no longer zigzag, there they are in blackish grains placed in rows along the passage-way. One may gather from these observations that the excreta of our insects are not of the same consistency at all ages, for when they were young they seem to have ejected material in an almost liquid state and later this in the form of grains which then must have had more solidity as they came out.

Our caterpillars do not enter the ground to transform, nor do they remain in the leaves where they have hitherto lived. When this critical time arrives (which is ordinarily in the middle of October) they quit their tunnels; they pierce the upper membrane and walk out on the leaf. They walk hither and thither, seeking a suitable spot in which to undergo transformations. Those that

I had shut up in a little box[2] chose the angles between the sides and the bottom and cover of the box to spin cocoons. I went out at once to examine the branches and stalks of the rose-bushes, in the leaves of which I had noticed empty mines, in order to discover the natural and unusual retreats of the insects. I found a good many of them enclosed in cocoons which were ordinarily placed in a chink or crevice of the bark of the stalks. Often they are found in the angles with the branches made with one another or in the angle formed by a large thorn with the branch to which it is attached. The caterpillars chose such places because they find it easier to fasten the threads of the cocoon all around their bodies in such a place; a flat surface would not be so suitable.

The cocoons in which they enclose themselves are oval and of a white color; the white of some of them borders on yellow. Although the walls are thin, they are closely fitting and very strong and one can hardly tear them open without wounding the insect within. In order to get the insect out of the cocoon without hurting it, it is necessary to use very fine scissors. I have often seen the caterpillars begin and complete their cocoons, but their work has nothing peculiar about it. . . . . As their bodies are supple they can bend and turn them in every way. It is easy to fasten threads on all sides, to reinforce them and finally to make cocoons of them.

In the cocoons they very soon take on the form of chrysalids of a fine yellow orange color, on which the parts of the future adult are marked more distinctly than on ordinary chrysalids. Their shape is oval. The abdomen which terminates in a truncate cone is divided into segments. The sheaths which cover the wings extend nearly to the end of the abdomen and have considerable width. The antennae and legs are arranged in the usual order between the wings.

It was not till June of the following year that I had occasion to see what had become of my little miners. I found them changed into winged insects; but what insects?—into Ichneumon flies. They had pierced in the cocoons little circular holes which had gained them their exit. This discovery struck me with astonish-

[2] "Poudrier"—sand or dust box from which the sand was shaken to dry ink as a blotter.

ment, I could not persuade myself that this was the natural transformation of my mining larvae. I was ignorant that often Ichneumon flies proceed from larvae which have themselves lived in the interior of caterpillars of other larvae bigger than themselves.

Happily a single insect of those which I had kept taught me the true form that they take on; among the little Ichneumons I found one insect of another form, in a word a true moth. It had certainly come out of the cocoons. I could have no doubt of it.

Very long ago the smallest of moths came to be designated as Microlepidoptera; the leaf-miners are the smallest of the micros. In this group the early systematists adopted the playful habit of appending the diminutive termination *ella* to each name of a species. This habit has continued down to this day, and has resulted in an excess of length to the names of these tiny creatures.

LIFE CYCLE

The life cycle of these miners is completed in a year at longest,[3] but many species have two or more generations annually.

The egg. The eggs of lepidopterous insects, though the diversity of their form is very great, have a tendency to be striated or ribbed. Frequently the micropylar area, the part of the shell where the sperm enters to fertilize the egg, is distinctly differentiated from the remainder of the egg surface. If that axis of the egg which passes through the micropyle is at right angles to the surface on which the egg is deposited the egg is said to be of the erect type, but if it is parallel with that surface it is of the flat type. In the leaf-miners most of the eggs are of the flat type, but in the case-bearers of the genus Coleophora the eggs are erect with the micropylar axis very much shortened. The eggs of the Microlepidoptera are very small, and little noticed, and for that reason few have been described.

[3] *Recurvaria milleri* takes two seasons to mature.

The females of a few of the most primitive genera are equipped with an ovipositor by means of which they are able to make punctures and to insert their eggs into the leaf tissue. We cite two of the best known examples.

The egg of *Eriocrania semipurpurella* is described by J. D. Hood as being cylindrical, twice as long as broad and rounded at the ends at the time of laying. Afterwards the egg swells and comes to fill the pocket in which it is, thus losing its symmetry. He gives the measurements of T. A. Chapman which show the ratio of the cubic contents at the

Fig. 20

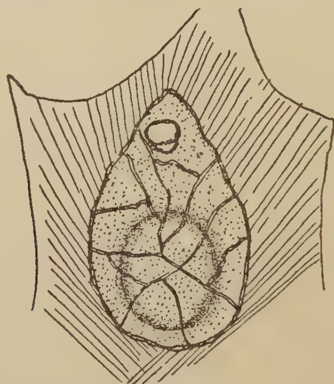


Fig. 21

Fig. 20. The ovipositor of the moth of the maple casebearer. (From Herrick.)

Fig. 21. The egg of maple casebearer in pocket on the under side of a leaf. (From Herrick.)

time of laying to the cubic contents on the fourth day thereafter to be as four is to eleven, the length at the time of laying being 0.0141 inch.

The eggs of the maple case-bearer *Paraclemensia acerifoliella* and the manner of their deposition are described and illustrated by Professor G. W. Herrick as follows:

The female moth deposits her eggs in tiny pear-shaped pockets in the tissues of the leaf just beneath the lower epidermis. The female has a complicated extrusile ovipositor. There are four

long, highly chitinized pieces, the members of the inner pair of which fuse at the distal ends and form a somewhat bell-shaped object with a sharp projecting point on the outer end (fig. 20). With her body as a fulcrum she bores a tiny circular hole through the epidermis and forms a pear-shaped pocket in the tissues. In the larger end of this she places the egg (fig. 21). Many eggs are deposited in a single leaf, often in chain-like rows of from three to six or even more. The tiny scars are conspicuous from the under sides of the leaves, and give a yellowish stippled effect from the upper sides. Egg deposition extends over a period of several days.

The egg is soft, white, and elliptical, and measures about 0.45 mm. in length, and 0.34 mm. in width, and 0.24 mm. in thickness. It is very soft, almost jelly-like, and not easy to dissect out. It probably hatches in about a week.

The eggs of Nepticula, Lithocolletis and many others that are placed on the surface of the leaf are domed above and flat on the side toward the leaf. From the traced impression on the egg surface of the tiny veins on which they lie, one may gather that the shells are soft and plastic at the time of laying.

There is great variation also in the position of the eggs on the host plants. Of the upper or lower leaf sides some persistently choose one and some the other surface and may even more particularly limit the position to near or away from the midrib or margin. Thus J. H. Wood writing of British Nepticulae says that of the forty-one species whose egg-laying habits were known to him, only four were inconstant in their choice. Of those four one frequenting two host plants placed her eggs on the upper side of the leaves of one and on the underside of the leaves of the other, seemingly on account of the character of the surfaces. Of this discrimination he says

Very commonly . . . . no explanation for the placing of the eggs is possible, beyond the simple statement that it is the nature

of the insect to place them where she does. For example, one species will lay on the upper side, and another, for no apparent cause, on the under side of the same leaf, and yet each will cling to its own habit as it were a matter of vital importance.

In hatching the larvae of some miners come through the egg shell on its exposed surface and afterwards burrow into the leaf, but a larger proportion burrow through the egg shell and into the leaf in one operation. Some larvae, especially those of the family Gracilariidae, are able to eat only in the plane of the long axis of their bodies; and it is only by virtue of their purchase on the egg shell and by taking a diagonal path into the leaf that they are able to effect an entrance. Nepticula has not the limitation of early "Gracilarian" head-parts, but the head has so come into alignment with the body and is so sunk into the prothorax that it would be equally helpless to enter a leaf from its surface. The Coleophorae, case-bearers, seem quite capable of eating at right angles to their bodies: and of those that are miners, some, as *Coleophora laricella,* bore from the egg directly into the leaf while others, as *Coleophora fletcherella* are naked exposed larvae for several hours. There is probably advantage in leaving no open door in the dwelling for the admission of such unwelcome guests as fungi and bacteria.

The larva. The larvae as they issue from the eggs are very minute. The number of times it is necessary for them to shed their skins to allow for new growth varies with genus and species and possibly at times even with the individual. Lithocolletis "of the flat group" (the Cameraria group) is said to moult seven times, while Nepticula moults three or four times. These probably represent the extremes of variation in this order, in which five is the usual and ordinary number of moults.

The form of the various leaf-mining larvae departs more or less widely from that of free-living caterpillars. Judged

by numerical abundance, success in leaf-mining seems to be directly proportional to the extent of modification. Probably modification has been by losses of parts more often than by accessions. Spines, for instance, would be almost prohibitive and are not to be found, even the setae being exceedingly small. The body has become flattened, especially in early instars of the sap feeders. As though to compensate for the decrease in height, the segments in many cases have become bulged out at the sides. From above, each larvae have something of the appearance of a chain of beads.

Well developed legs are not much needed where there is little distance to go and scant room to go in. Hence we find the legs in all stages of reduction from fairly well developed to entirely wanting. Eriocrania have larvae that are entirely footless throughout larval life; so, also have Heliozela and Antispila. Phyllocnistis has no legs corresponding either to the thoracic legs or to the prolegs of other caterpillars, but slanting downward from the sides of each abdominal segment except the last are membranous outpushings of the body wall, homologous, not with prolegs, but with the mamillations at the sides of the segments of other mining larvae.

In free-living caterpillars ordinarily there are three pairs of horny segmented thoracic legs and five pairs of fleshy abdominal legs; i.e., prolegs on abdominal segments 3, 4, 5, 6 and 10. The prolegs are usually provided with a band or circlet of hooks or "crochets" whose arrangement and form differs sufficiently to make them a useful character in classification. Chapman was the first to call attention to the fact that the crochets of "Micros" are usually arranged in a simple or multiserial circle while those of the "Macros" are usually placed in a longitudinal row.

Between the footless condition mentioned above and the typical sixteen-legged caterpillars there are among the

Microlepidoptera and especially among the leaf-miners very many intermediate forms. In these, the prolegs may be indicated only by the presence of crochets with all indication of a swelling lacking or the reverse.

In some families (Tischeriidae, Gracilariidae), these crochets may be found representing the prolegs while thoracic legs may be entirely wanting. In the former family thoracic legs are never present and the crochets are found on segments 3, 4, 5 and 6 of the abdomen. In the Gracilariidae, however, thoracic legs are present in the Gracilarinae, present or absent in the Lithocolletinae, but the prolegs represented by crochets or modified into suckers, appear only on segments 3, 4 and 5 of the abdomen, a feature not found save in this family.

Nepticula has neither segmented thoracic legs nor crochets, but there are present fleshy leg-like swellings on segments 2 and 3 of the thorax and segments 2, 3, 4, 5, 6 and 10 of the abdomen.

In some cases the prolegs are reduced though the thoracic legs be well developed. Thus, in the genus of case-bearers, Coleophora, which, after their leaf-mining infancy is past, will walk around on their thoracic legs bearing their abdomen and its enveloping case aloft behind, the thoracic legs have need to be stout but the prolegs are in all stages of reduction until in *Coleophora limospinnella* the crochets are lacking entirely. In the case-bearers there is also the tendency for the two rows of prolegs to approach one another on the mid-ventral line so that the crochets which are all of one size and in one row will form nearly continuous transverse bands. In some of the mining Gelechiidae also the prolegs are much reduced.

In Bucculatrix the prolegs are long and slender, but this accords with the fact that Bucculatrix is a miner for but a short time, and the long prolegs become useful in the course of external feeding.

Leaf-mining influences the shape of the head-capsule no less than the form of body and the development of legs. In free-living caterpillars, the three principal parts which make the head-capsule, namely, the right and left sides and the front, are separated from one another by a Y-shaped

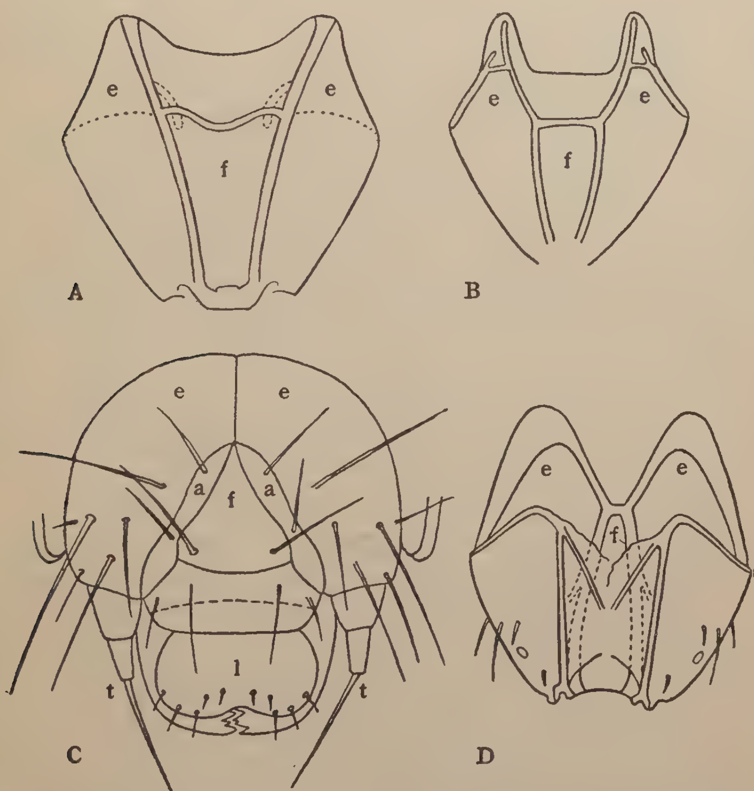


FIG. 22. Alteration of form of head capsule and mouth parts in leaf-mining caterpillars. (After Traegardh.) *A* and *B*, head capsules of two sap-feeding leaf-miners, Lithocolletis and Phyllocnistis respectively: lettering as before. *C*, the head of an ordinary caterpillar, face view; *f*, frons; *a*, *a*, adfrontal pieces; *e*, *e*, epicronial plates, separated by an epicronial suture; 1, labrum partly covering the mandibles; *t*, *t*, antennae. *D*, head capsule (appendages omitted of a tissue-feeding leaf-miner, Aphelosetia. The frons reaches backward to the rear margin between the prolonged epicronial plates.

suture. The front is usually a triangular sclerite above the mouth parts (*f* of fig. 22 C). Between it and the large side sclerites are two small sclerites, called ad-frontal pieces (*a*). In most free-living caterpillars the sutures bounding the sides of the front meet halfway the epicranial suture which separates the two sides. In some leaf-miners the ad-frontal pieces disappear, the front extends far back and the arms of the Y do not unite to form a stem. In such a case the front is said to be "open."[4]

The researches of Ivar Traegardh (1913) have especially pointed out the effect of the leaf-mining habit on these sutures and their correlation with the flattening of the head-capsule. From narrow deep sutures they become broad shallow ones. From sutures meeting one-third or one-half the way forward, they here meet first at the hind margin, the vertical angle of the head; or indeed they may not meet at all but may be joined by a bridge which increases in length as the sutures become more nearly parallel to one another. In the sap-feeders these sutures actually diverge posteriorly.

Besides the change in the relations of the sutures, there is the difference in the angle which the head makes with the axis of the body. In external feeders the dorsal side of the head is longer than the ventral but the hind margins are in nearly the same vertical plane since the head is bent obliquely downwards. In the leaf-miners, on the contrary, the head-capsule becomes horizontal.

In the tissue-feeders this change is brought about by having the hind parts of the dorsal side of the capsule withdrawn into a fold of the prothorax, and at the sides the hind margins have developed into thin blades, enormously expanded to rearward for muscle attachment. These forms feed by actually tearing out and swallowing mouthful

[4] The sutures must not be confused with the tentatorial arms which show more plainly than the sutures in microscopic preparations.

after mouthful of the tissue in the path forming a real tunnel that allows considerable vertical space for moving.

The sap-feeders, however, shear through a single layer of parenchyma cells and suck their liquid contents, leaving the solid parts in place, there is indeed a premium on vertical space. The retraction of the head would give an obviously undesirable increase in height. The horizontal position of the capsule is in these brought about by the lengthening of the ventral surface so that the two sides of the head are of about equal length and then only the dorsal hind margin is overlapped by the prothorax.

In the sap-feeders not only is the capsule thin and free, but the oval outline of the head is completely abandoned. The lateral margins are almost straight, diverging backward. There is a blunt transverse front border from which the mouth parts project in such a way as to leave a right angled notch at either side for the insertion of antennae. This trapezoidal wedge-formed head is doubtless mechanically efficient in severing tissue after the unique fashion of the sap-feeders, and it is peculiar to these forms.

The eyes, also, are affected. This pronounced dorso-ventral flattening causes a sharp fold to occur in the head-capsule in that region where the ocelli are found in external feeding caterpillars. If no change occurred in their arrangement this would cause some of the six ocelli to be found on the dorsal side and some on the ventral side and directed towards the epidermis in either case. As Traegardh (1913) has remarked "it seems reasonable to suppose that the only direction in which there is any need for them to discern things is the only one in which they are moving, i.e., the horizontal plane." The problem is then seen to be to have them as nearly marginal as possible.

In full-grown larvae of Ornix we have the normal arrangement of ocelli in the free-feeding caterpillar, i.e., forward on the side of the head closely behind the base of the mandibles.

They are six in number, nearly uniform in size and arranged in a more or less regular semicircle which is opened posteriorly and subventrally. The difference from this condition is, in the leaf-miners, both in arrangements and number.

In getting them nearly marginal, Laverna has five ocelli in a rather straight line near the edge, with the foremost of the five and a sixth one that is farther from this line on the very margin. Cemiostoma has all six in a zigzag line on the dorsal surface near the margin. Aphelosetia has but five all very near the margin, three on the dorsal and three on the ventral surface. In *Tischeria eikbladhella* all are in one row but the three anterior ones and the three posterior are grouped in sets.

The tendency to reduction in number is carried further in some species of Lithocolletis where in the young larvae five of the six ocelli present are all much reduced in size. In other species of this genus young larvae have but four ocelli. In Eriocrania and Nepticula there is one large ocellus only.

The antennae of leaf-mining caterpillars are reduced to a greater extent than are those of external feeders. Traegardh has traced the stages of their reduction pointing out that loss in segments may begin at the proximal or distal end. The antennae of tissue feeders are more reduced than those of sap-feeders. This is doubtless correlated with the insertion of those of the latter in the necklike constriction between the head-capsule and the mouth parts. In these lateral incurvations they are but slightly exposed to pressure against the walls of the mines.

Mouth parts. But if the effect of leaf-mining is impressed on the form of body and the locomotor appendages, in the shape of the head-capsule and its sensory organs, it is nowhere more apparent than in the mouth parts, especially in those of the early sap-feeding instars of the Gracilaridae. From the condition in ordinary caterpillars—a labrum shaped as a transversal plate, mandibles as triangular or

quadrangular plates convex on the exterior concave on the interior side, maxillae with well developed palpi and a labium or lower lip also with palpi,—from this condition it is a far cry to the mouth parts of the feeding stages of Phylloconistis and the early instars of Gracilaridae.

The difference consists not only in the different size, form, and degree of development, but in the apparent presence or absence of some of the organs themselves. Here the

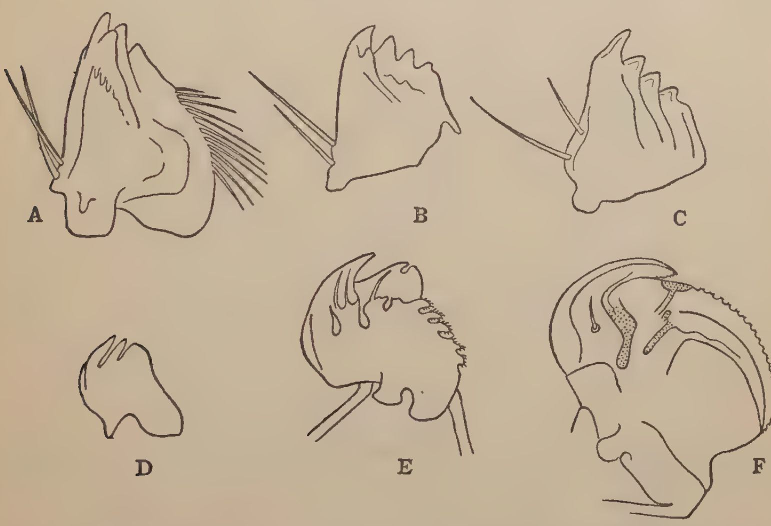


FIG. 23. Mandibles of leaf-mining caterpillars. (After Traegardh.) *A*, Tischeria; *B*, Nepticula; *C*, Cnemiostoma; *D*, Parornix; *E*, Lithocolletis; *F*, Phyllocnistis.

mandible becomes an extraordinary structure, looking considerably more like a circular saw and working in a way more similar to that of a saw than of an ordinary mandible. Here it is a flat disc hinged at its proximal border and working to and fro in a horizontal plane. Enclosing the mandibles are two thin flaps. The one that is above is the labrum considerable enlarged, the one below is similar to it and is made up for the most part of the maxillae, labium

and the hypopharynx. These together form a sort of sheath in which the saw edges of the mandibles move back and forth. They cut through the cells and set free their juices which are then sucked in through the sheath or funnel and are swallowed.

Even in such tissue-feeding forms as Aphelosetia and Nepticula there is reduction or modification of the spinneret and labial palpi, an increase of the hypopharynx to form a

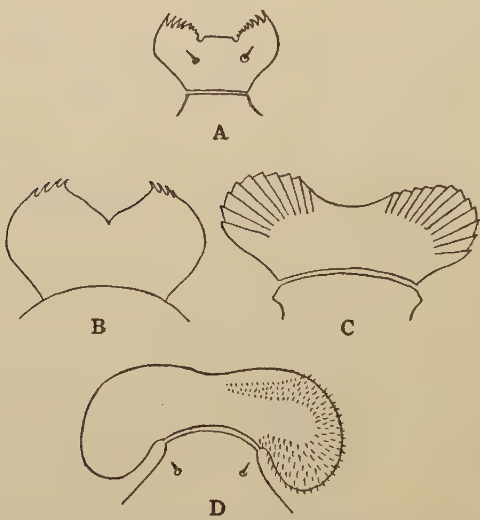


FIG. 24. A series of labra of sap-feeding leaf-miners. (After Traegardh.) *A*, Parornix, *B*, Gracilaria; *C*, Lithocolletis; *D*. Phyllocnistis.

flat lamina and a great increase of the stipes of the maxillae; but in the sap-feeders these specializations are carried to the extreme, so that while several organs, as the mandibles, labrum, hypopharynx and labium, have attained a very considerable size, others, as the maxillary and labial palpi and the spinneret, are almost or entirely atrophied. The condition is one of the most unique in the insect world.

Pupa. As in the larva, so in the pupa, we find a curiously

interesting and varied assortment of forms in the leaf-feeding Lepidoptera. Of these perhaps the pupae of the Eriocraniidae are the most surprising. In Eriocrania the pupal skin is soft and the various parts are hardly fused together at all. In emergence the head is free to move, the face is lifted up, the jaws (curiously developed and functional structures here, see p. 76) open to pass each other.

In other pupae there are varying degrees of fusion. Some are nearly as free as these Eriocranids, and some are completely fused and quiescent. Among leaf-mining Lepidoptera we find these two extremes and most of the intervening forms. Thus in Nepticulae, which are primitive, the first six abdominal segments are all free. In Incurvaria the first of these is fixed and soldered with the thorax and so are the first two of them in Tischeria. In Bucculatrix the first two are fixed and the third is nearly so. In the mass of species of the Microlepidoptera the first three of these segments are fixed. In the Gracilariidae the first four abdominal segments are fixed but the fifth and sixth (and seventh in the males) are free. Between these and the entirely quiescent pupae, transition forms are lacking save that in the Lyonetidae the parts of the immovable pupa are more feebly fused than in the typical "obtect" pupae, and in some Gelechiids only dorso-ventral movements are possible.

In the Gracilarids and all the forms having a lesser degree of fusion than these, the pupae are more or less active and twist about when they are disturbed in any way. As in Eriocrania the pupal skin is worked out of the pupal case before the adult emerges. This is accomplished by the movements within the pupal case of the fully-formed adult abetted by ingenious modifications of the pupal case itself. In Lithocolletis and others the top of the head, which is sharpened almost to a beak and often supplied with a toothed crest, makes an excellent ramming tool, while on the dorsal sclerites of the abdomen are patches of small stout

backwardly-directed hooks which serve as an anchorage, and hold in the passage through the cocoon wall. In Eriocrania the structures which accomplish the same ends are chiefly the great mandibles which work back and forth to burst the cocoon and then to dig up through the soil.

Adults. The adults of leaf-mining caterpillars are nearly all very small. Some members of the genus Nepticula have a wing expanse of hardly 3 mm. ($\frac{1}{8}$ inch), and the average expanse of wing in the great genus Lithocolletis is between 5 and 8 mm.

But for all their minuteness the "micros" are creatures of exquisite beauty. It is as though having so little area they could be prodigal in decoration of it; they are lavish of silver and gold, of color and design. As Reaumur writing almost two hundred years ago says of them "Nature would have nothing more rich, nothing more brilliant, nothing more beautiful than such moths had they been built on a large scale." Very often the hind wings are very lanceolate with fringes as wide as or wider than the wing. In most, the fore wing is the one on which the color pattern is elaborated. This wing, too, is often very much fringed. In the various families the clothing of the head, the shape and position of the palpi, and antennae, length of the tongue, and especially the venation of the wings varies very much, as may readily be seen from looking over the fine hand-colored plates in Stainton's *Natural History of the Tineina*, or the line drawings in Spuler's *Schmetterlinge von Europa;* but in this discussion it is with the habits of the larvae rather than the characters of the adults that we are particularly concerned.

THE MINES

If individuality is to be found in the forms of these creatures in their various stages it is even more apparent in their manner of life. Frequently though the insect itself may not be seen in any stage, chapters of life history written in green

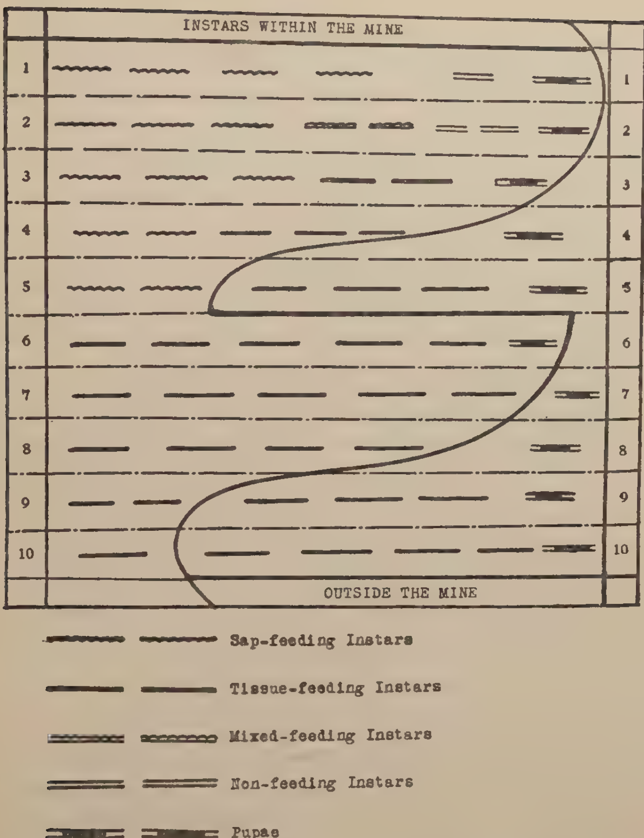


FIG. 25. Diagram of leaf-inhabiting stages in certain Lepidopterous larvae. Read from the bottom upward; it is also a diagram of progressive adaptation. The upper half of it represents the Gracilarian (sap-feeding) series. Line 1 represents Phyllocnistis only. Line 2 represents typical conditions among the second (Cameraria) group of Lithocolletis—the group with flat larvae. Line 3 represents the first (typical) group of Lithocolletis larvae (except *L. ostensackenella*). Line 4 represents Leucanthiza, and Apophthisis, and typical Acrocercops. Line 5 represents Gracilaria (in part), Parornix and others. Line 6 represents Paralechia. Line 7 represents Proleucoptera, Leucoptera, Lyonetia, Aphelosetia, Cycloplasis, and others. Line 8 represents Nepticula (*teste* Miss Braun). Line 9 represents Nonagria and others. Line 10 represents Arzama and others. Most important of the others in the last two cases (lines 9 and 10) are two large genera whose species are not quite uniform in leaf-mining instars: Bucculatrix, whose larvae later feed openly upon the leaves, and Coleophora, whose larvae later are mainly case-bearers. The diagram is not exact; it is intended only to show the general trend in evolution of the leaf-mining habit.

leaves for all to read will speak more plainly than an adult caught on the wing or a larva pickled in a bottle. These last are objects on which systematists and anatomists can do and have done careful and useful work; but the mines in the leaves confront even the casual observer; sometimes they affect economically the gardener, the fruit-grower or the farmer; and they are things of absorbing interest to the general naturalist or ecologist.

Tenancy. In life habits mining caterpillars differ from one another in the proportion of their immature stages given over to living in mines. Some are miners but for a short part of their larval life, afterwards emerging to feed outside; some spend all of their larval life in the leaf but emerge to pupate, while still others spend all larval and pupal stages in the mine and emerge first as adults. The accompanying diagram will illustrate these differences, together with the relation they bear to sap-feeding and to tissue-feeding habits.

Most of those that leave the mine as fairly young larvae have some definite shelter during the remainder of their feeding stages. Parornix and Gracilaria, for instance, spin a web to fold or curl the leaves, and then feed within the chamber so made. Most of the mining Gelechias either fold the leaves or web several leaves together in late larval life. *Scythris matutella* according to Chambers makes a web on the under side of the leaves of Giant Ragweed, *Ambrosia trifida,* and mines from this shelter in small patches. *Gnorimoschema scutellariaella* similarly, is said to make a shelter of silk, but here in the shape of a tube or case covered externally with frass. From the narrower end of this case it passes into the interior of the leaf of the skull-cap, *Scutellaria lateriflora,* to feed.

The Coleophoras, case-bearers, as their names suggest, make cases by cutting out and sticking together portions of the walls of the mine. These instead of being fixed and stationary as in the *Gnorimoschema,* are portable.

Of all the species that leave the mine as young larvae, those of but one genus, namely Bucculatrix, feed openly and quite without shelter of any kind. Danger of evaporation is probably very real for small larvae, and in these the shaggreening of the body surface is doubtless a compensatory adaptation. At the time of moulting even these spread silken nets for cover ("moulting cocoons"), and emerge again to feed when their new cuticles are a little hardened.

Of those miners that leave the mines only when they are fully grown some, as Nepticula, Coriscium, Phthorimaea, Cemiostoma and others, make a hole in the cuticle and slip through it as naked larvae. They seek out safe places in crevices of bark or among the debris on the ground and spin their cocoons.

Some few miners as Aphelosetia and Bedellia, for example, pupate just at the door of their mines attached to their host plant by a very few strands of silk without any particular protection or covering, as naked, pupae.

There are other miners which do all their feeding within the leaf and then carry away a bit of the mine in the form of a case. This case is made like that of the case-bearing Coleophoras, but in Antispila, Coptodisca, Heliozela, and the European genus Phylloporia the case is used only as a pupation cell and not for feeding. Cycloplasis has evolved a slightly different method of making a pupating case from leaf cuticle. This it does by cutting out a larger circular disc from one cuticle only, and then folding this disc along a diameter and sewing one semi-circular edge to the other one to make a half moon shaped case. These fall to the ground with the larva inside, and here pupation takes place.

There remains the consideration of such miners as feed and pupate without leaving the leaf. Phyllocnistis pupates in a bit of a "nidus," a silk-lined pocket but little wider than its linear mine and usually at the edge of the leaf. Tischeria pupates in the mine, some species lying free on

the silk carpeted floor, others, in a special cocoon attached to the upper surface. In the large genus Lithocolletis, in so far as habits are known, all our species but one (*L. ostensackenella*) pupate in the mine.

All the forms of mines mentioned in our introduction (p. 12) are made by Lepidoptera. There is a general correlation between the type of mine and the genus. There is also probably a correlation between the form of the larva and the form of mine, Nepticulae, as a rule, make linear, serpentine mines which later may or may not become blotches. Phyllocnistis always makes a very long, tortuous linear mine which does not become a blotch. Bucculatrix always makes a linear serpentine mine during its early life. It is interesting to note that these three have structures which would seem well adapted for forward movement: These feed in arcs, swaying the anterior part of the body from side to side and getting some impact against the parenchyma by alternately stiffening and relaxing the body.

There are differences among mines that are perhaps more significant than that of superficial shape. Of linear mines, for instance, those of the genus Phyllocnistis can almost surely be identified at sight. This is a genus of sap-feeders and practically none of the parenchyma is removed but the superficial layer of these cells is sheared through and the liquid contents sucked up. In this respect the mine does not change from beginning to end. On account of the liquid diet the mine is affected in several ways. In order to collect enough food from sap alone to make a whole moth, be it ever so small, it is necessary to use quantities of the sap and, therefore, the mine is very long indeed. Then so little of the leaf substance being removed, there is almost no difference in transparency between the mined area and the remainder of the leaf. Then the castings, if they show at all, do so only by reason of their changed color or because they make the cuticle to adhere again to the parenchyma

for it is obviously impossible to get much nourishment from sap and still leave anything particularly solid in the excrement.

The mines of Nepticulae begin as slender galleries and often continue so until the end but these are readily distinguishable from the linear mines of Phyllocnistis. Nepticulae are tissue feeders and tunnel out much parenchyma, thus leaving the mined area more transparent than the remainder of the leaf. There is very much more body to the excrement. Sometimes Nepticula mines widen out into a blotch and this widening may be quite abrupt, synchronous with the last larval moult.

Members of the genus Bucculatrix make narrow winding galleries; but because they become external feeders early in their life history their mines may be recognized by their shortness especially if small scars halfway through the leaf show where they have fed externally.

Of the blotch mines, the mines of Tischeria usually start as a narrow channel but almost at once they begin to widen and presently spread out as a great blotch. Certain of them that widen out and gradually to a flaring edge have been called trumpet mines. They are rather unique in being carpeted throughout with silk.

While the mouthparts of the Lithocolletis larva are adapted for sap-feeding it shears loose the epidermis over the whole territory of its mine. When at the third moult it acquires tissue-feeding mouthparts it goes over the same area again this time carefully stripping the mesh of veins of all parenchyma. With these mouthparts comes also the ability to spin silk, an ability which some of them employ in making their quarters more roomy in keeping with their now cylindrical form. They spin the silk back and forth over the loosened cuticle of the leaf and this silk in drying shrinks, drawing the cuticle into folds. The other thicker side arches in proportion and the erstwhile flat mine is con-

verted into a spacious chamber. Mines so made are called tentiform mines. They usually occur on the lower side of

Fig. 26. Leaf of the Western Sycamore, *Platanus occidentalis*, with three mines of the moth, *Lithocolletis felinella* as found in December. Beyond each mine is a blotch of green in the brown leaf, giving a variegated appearance to the whole tree.

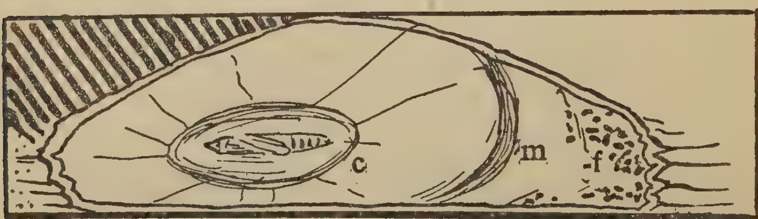


Fig. 27. Diagram of one of the mines shown in figure 3. *c*, cocoon containing pupa; *m*, midden-screen of silk; *f*, frass.

the leaf of the host plant, that is, the cuticle is first loosened on the lower side.

The larvae of the second group of Lithocolletis, the Cameraria group, loosen the upper epidermis of the leaf. After their third moult their head capsules and bodies are still very much flattened and instead of having the head then at a slightly oblique angle to the body as in Lithocolletis proper, it continues to lie in the same plane. This structural difference is accompanied by a difference in habit. Instead of feeding within the limits of the mine already made they go on increasing the area of the blotch (or gallery as it may be) by eating further into the leaf, now ingesting thin slices of the tissue instead of merely shearing through cells to take their sap. One often meets certain unique types of mining. The senior author has studied the western sycamore miner, *Lithocolletis felinella*. The larvae in feeding cut the fibrovascular bundles in such a way that the portions of the leaf beyond the mines remain green after the rest of the leaf has turned brown.

FRASS DISPOSAL

If there are advantages to these tiny caterpillars in being shut up within a thinly spread but dependable food supply out of danger from evaporation and from the clumsier of their predaceous enemies, there is also the disadvantage of being close-quartered with their own waste. That it is a disadvantage to them may be guessed from the pains they take to dispose of their frass; and the constancy and precision of miners in this respect is one of the best clues to their identity. If the mine be linear the problem is simple. The frass is left in a trail behind; the food is ahead and uncontaminated. Some miners, usually those making blotches, go to the trouble of making holes for ejecting the frass out of the mine. Thus the species of Cosmopteryx make small round holes at intervals for the purpose. Some species of Tischeria make slits on the lower side of the leaf. *Bedellia somnulentella*, after making a linear mine as a young larva,

leaves this mine when about 2 mm. long, and, entering between the cuticles of the leaf of the common morning glory at another point, makes a blotch mine but it either leaves the posterior segments of the body extruded or it returns to the entrance for the purpose of ejecting frass. *Parectopa robiniella* makes a digitate mine on the upper surface of the leaf of black locust but it enters the leaf from the lower side, making a very small mine there and then passes up through the plane of fibrovascular bundles to mine under the upper cuticle. It keeps returning to the hole into the lower side mine to stuff its frass down there. Sometimes its cast skins may be packed in with the remainder of its waste. Those superb miners, the Gracilaridae, do not eject excrement from the mine but the ingenuity some of them show in otherwise getting it out of the way is interesting. For example, *Lithocolletis lucetiella*, mining the lower surface of basswood trees, during its early instars while it has sap-feeding mouthparts, carefully shears loose the lower epidermis, feeding on the liquid contents of the cut cells. The excreta of this period are so small in amount as to be unimportant. After the third moult when tissue feeding mouthparts are acquired the caterpillar does not extend the mine but goes back over this rectangular vein-bordered blotch, eating as it goes every vestige of parenchyma and leaving a splendid dissection of the fibrovascular network. Now the amount of undigested material is increased very much and the problem is to dispose of it with the least possible contamination of the food supply, for by taking all the parenchyma in that scant area there is none too much to bring the larva to full growth. This is the solution: The larva begins eating at the very edge of the mine and eats all the way around the edge first and then gradually in toward the middle. By the time the first frass pellet is ready, there is a narrow space at the edge where the larva has just been eating that is entirely stripped

of food and there the pellet is deposited. As the larva continues to eat it continues to deposit its frass pellets at the extreme periphery of the mine and in a place from which the parenchyma has been removed. Not a scrap of parenchyma is wasted and when the larva is mature the tiny round black frass pellets are tidily ranged round the edge while the central part is immaculately clean. Even the moult skins may be pushed back with the remainder of the rubbish. In the geometrical center between the two white and transparent cuticles of the mine the fastidious larva spins a shining transparent pupating chamber.

Antispila isabella mining in grape leaves in September collects its excrement at one end of the mine on the floor. In cutting out a case it chooses that part of the mine farthest from the excrement.

Many other larvae either find contact with their frass less objectionable or they are less clever in avoiding it. Some of them web it together with silk to make a tube into which to retire from feeding. Many employ it in making their pupal cases, either outlining the chamber with it as does *Lithocolletis basistrigella*, or to strengthen the walls as does *Lithocolletis ostryaefoliella*. In the group of Cameraria (flat group Lithocolletis larvae) the food is taken in very thin slices even after the third moult and the proportion of sap is therefore high. The frass is consequently very fine grained and rather fluid, and instead of being formed into firm pellets, it is spread unevenly about in a waxy layer over the floor of the mine.

Silk spinning. In many leaf-mining larvae the ability to spin shows itself only in constructing a cocoon either pupating or hibernating. Some few tissue-feeders, as Antispila, Coptodisca, etc., line with silk that portion of the mine which they later remove as a case. In the Gracilariidae the spinneret does not show itself until sap-feeding is over and the second form of mouthparts is assumed.

The larvae of Tischeria spin as they mine, lining their passageways with silk throughout. Gracilaria and Parornix use silk in curling leaves. Lithocolletis larvae by its use make a vaulted mine of a flat one.

Thus we see there are many clues to the identification of Lepidopterous leaf-miners; but they are a host and with all these clues their determination is not always easy. The first and best clue is the name of the plant on which the mine is found. Our index of host plants with lists of the miners that are known to infest them should help here. Then there is the form and color of the mine and of the larva or pupa, the nature and arrangement of frass and of silk; and finally cast skins, particularly the brownish head capsules, may often be found in mines, even though the mine-maker be departed, and these may assist in establishing the identity of the erstwhile tenant.

CHAPTER IV

SUBORDER JUGATAE

SMALL-WINGED JUGATES

In Stainton's time and even until Comstock's work on wing venation in 1893 the small-winged Jugates were usually associated with the other very small Lepidoptera of leaf-mining habits under the old, comfortably inclusive denomination of "Tineina." Stainton speaks of these forms as "allied to Tinea." Still, in the light of the present disposition of the group, his further remark is interesting. He says, "the similarity of the neuration of the anterior and posterior wings, analogous to what we find in Nepticula, is curiously accompanied by a shortness of antennae in both these genera; *strange, too, that both peculiarities are given combined in Hepialus.*" Herrich Schaffer, in his *Schmetterlinge von Europa* removed them entirely from the position they had held among the Tineina and placed them as a distinct group, Micropterygina, at the very end of the Lepidoptera.

It remained for a later worker (J. H. Comstock) to add the weight of further evidence from the study of venation, before either of these suggestions were generally heeded; but now the Micropterygidae are associated with the Hepialidae, and in a separate suborder, not only from the Tineina, but from all other known Lepidoptera. They are also at the "end of the Lepidoptera," but it is the more primitive end. They may therefore be considered first.

The characters which distinguish these, the Jugatae, from all the rest, the Frenatae, are "the jugum" for interlocking the wings in flight, the fact that the fore and hind wings are

alike in venation, remote from one another at the base, and semi-oval in shape and that the fore wings are marbled or reticulated.

FAMILY ERIOCRANIIDAE

The leaf-mining members of the Lepidopterous suborder Jugatae are but a few species comprising the small family Eriocraniidae. *Eriocrania auricyanea,* has been carefully studied by August Busck (1914), who describes the adult as "a small (expanse 12 to 14 mm.) strongly iridescent golden bronze moth, sprinkled with scintillating, bright metallic purple scales." European species were studied earlier in England by Chapman (1900). The following account is mainly based on the work of these two authors.

Eggs. The rounded cylindrical eggs are placed in a pocket, cut in the tissue of a leaf by a serrated, lancet-like implement in the abdomen of the female. J. H. Wood describes the process for the European *Eriocrania semipurpurella.* The adult, he says, selected a "forward bush" of birch (*Betula alba*) just coming into leaf. She examined a bud with her maxillary palpi and finding it to her liking took a lengthwise position on a leaf. She then curved her abdomen and inserted the points between the folds. After a series of rocking and thrusting movements, with intervals of rest, the ovipositor was withdrawn. Going to other buds she made one laying in each. If the temperature was "warm" a laying took two and one-half minutes, if "cold" four minutes. Examination of the leaf made apparent a small incision on the underside which led to a deepish chamber with an egg in the bottom. Dr. T. A. Chapman observed the process in *Eriocrania purpuriella.* This species sits across the leaf and pierces it on the edge of a lateral rib. Her pocket is wider and shallower and usually contains three eggs. In "cold weather" it sometimes took her fifteen minutes to make a laying. According to Busck and Boving

the eggs of a native species, *E. auricyanea*, are laid singly near the edges of the opening leaves of oak, chestnut or chinquapin in April. In this case dissection of the abdomen shows that the number of eggs laid by a single female is about forty.

After the eggs of Eriocrania are laid they swell sometimes to more than twice their original size to fill the pocket. After a week to fifteen days the larvae emerge from the egg and begin to mine in the leaf. They are found particularly on species of the birch and oak families, i.e., birch, hazel, oak, chestnut, beech. The mine often begins as a gallery but soon expands to a blotch which may or may not involve the part of the leaf where the gallery was at first.

According to Busck and Boving this early part of the mine of *E. auricyanea* is normally obliterated, making a fissure in the growing leaf. Infested leaves may often be located by this fissure. The blotch becomes big and bulgy and is "suggestive of a sawfly or beetle mine." The entire parenchyma is eaten out and the mine is equally visible from both sides and so translucent that one may easily see the larvae and the black frass which is voided in long irregularly curled threads. By these threads of excrement one may almost certainly identify an eriocranid mine even when the miner has departed.

Larvae. The larvae are apodal. The full-grown larvae of *E. auricyanea* are 9 to 10 mm. long, whitish in color and somewhat flattened. The head is small. Segments two to four are broad and according to Meyrick have minute "subdorsal and supra-ventral" protrusible papillae. The fifth segment has lateral projections. It then tapers posteriorly to a very narrow anal segment.

Concerning behavior while mining, Kearfoot gives a brief account of an eriocranid larva which he found in the leaves of chestnut at Mont Clair, N. J. early in the spring of 1902. In this case history repeated itself in that Kearfoot, like the

European microlepidopterists before him, judged the larva to be coleopterous and so gave it scant attention. He did, however, take some notice of its behavior. He says that it mined in half circles of about 10 mm. diameter using the point of the anal segments as a pivot on which to swing, that it ate rapidly, and wriggled about very much if disturbed. The mines occupied sometimes the whole end of a leaf or half of one side of the midrib.

About the first of June he put some of the leaves in a container with some soil and a bit of moss and noticed that in a few days the larvae left the leaves and went into the soil. Afterwards reading in Stainton's *Natural History of the Tineina* he found a clue to their real identity and, returning with some avidity to the container, he found in the soil the tough typical cocoons and within them some dried up larvae and pupae but some living pupae also. These last he was able to identify with certainty by a comparison with Packard's figure of *Eriocrania purpurella* of Europe. He was, however, unable to breed the perfect insect and so to state with certainty its species. This Busck accomplished later.

The period of mining is very short. According to Busck and Boving the larva of *E. auricyanea* is full-grown about ten days after the hatching of the egg. It then cuts a small semicircular slit in the upper epidermis of the leaf and leaves the mine, dropping to the ground, where it at once digs down until it finds a suitable place in which to make its cocoon. Normally this is attained within a few inches or even less from the surface of the ground, often next to a stone, and there are records of depths as great as 8–10 inches. There the larva bends itself into a circle and pushes the soil aside to make a small firm cell in which it then spins its very strong oval cocoon.

The cocoon is so tight fitting around the larva and is made of so closely woven tough silk that it is difficult to cut it

open in any way without injuring the larva within. The coccon, in the case of *E. auricyanea* is about 2 mm. by 4 mm. and is made of whitish silk with small grains of earth and sand firmly incorporated in its surface.

All this is finished by about the middle of May. In this cocoon it then stays until the following April, a period of eleven months or more. This disproportion of the resting to the active period is the more remarkable in that for eight or nine of the eleven months it is in the larval condition apparently unchanged, the pupal period being relatively short.

It is not illogical, however, for meanwhile there are no enfolded, and very young uncutinized leaves for the insertion of eggs; nor young, soft growing leaves to be food for the larvae. When these conditions come again another generation is begun and not before.

Perhaps there is a connection between the long larval rest and the remarkable form of the pupa that is at length to be found in the cocoons. For whereas the head of the larva is small with mouth parts in proportion; and whereas the mandibles, in particular, of the adult are small, weak, and non functional, the mandibles of the pupa are—in proportion to the rest of it—immense structures; and they are functional, being used to tear open the strong cocoon and to dig a way out of the soil when the pupa is mature and ready for the emergence of the adult.

Pupae.—The pupa, like the larva, very nearly fills the cocoon. It has all appendages free and unfused and all the segments of the body are movable. The head especially can be moved up and down and sidewise. There is no room in the cocoon for these movements, but if a pupa be taken out and lightly touched with a brush, it responds, according to Busck and Boving, with a grotesque nodding of its head and with the swinging out of the enormous mandibles in a deliberate manner. Movement is particularly free in the

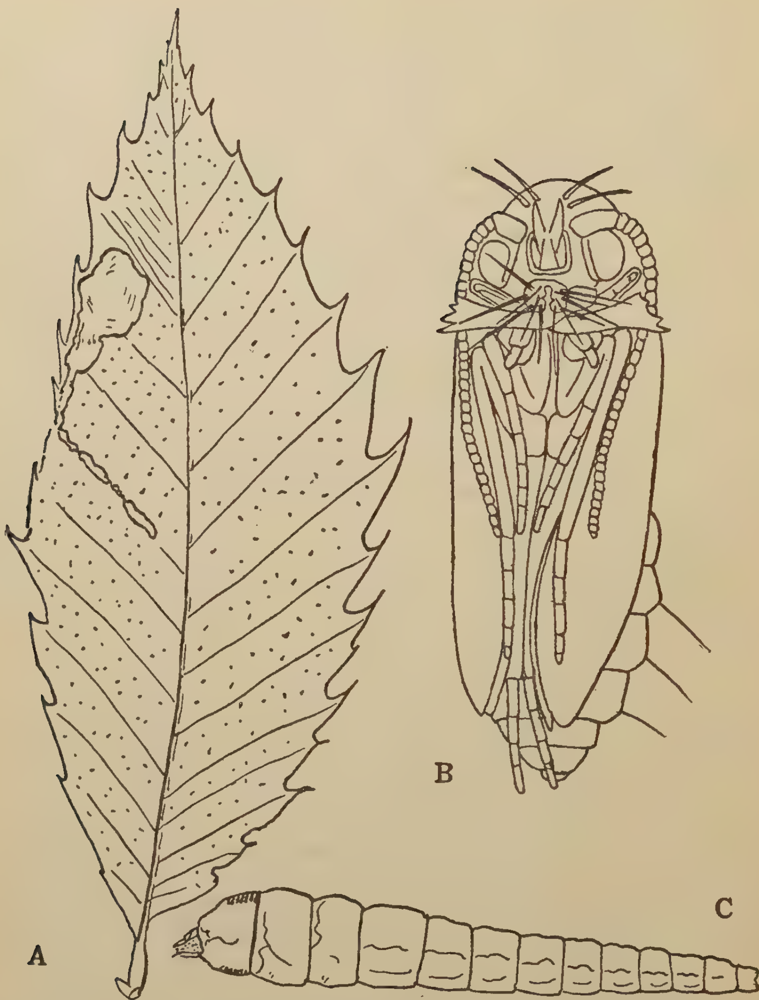


FIG. 28. The chestnut leaf-miner *Eriocrania auricyanea.* (After Busck and Boeving.) *A*, a chestnut leaf bearing a mine; *B*, a larva in lateral view, setae omitted; *C*, a pupa. Note the enormous crossed mandibles.

head, mandibles, and thoracic segments. T. A. Chapman examined and described the pupa of *Eriocrania purpuriella* and observed its emergence. His measurements will give

some idea of the proportion of the parts. The whole pupa is 4 mm. long and 1.3 mm. wide at its widest point. The head is 0.9 mm. wide and each mandible is 0.7 mm. long.

The only part of the pupa which is strongly chitinized besides the mandibles is the supporting mouth frame, an oval loop of chitin with which they articulate, the remainder of the pupal skin being exceedingly delicate so that the adult structures can be seen within. The arm-like mandibles (fig. 28 B) are firmly joined to the mouth frame. Their inner edge is sharply serrated nearly to the end and the apex is broadened out into a formidable club, the edges of which are armed with several strong teeth. They are moved by strong muscles identical with the abductor and adductor mandibulae found in insects with biting mouth parts. The abductor muscle enables it to make a strong outward swinging movement and this is used to tear the tough cocoon and afterwards to dig up through the soil. The small imaginal mandibles may be found in the bases of the pupal ones by dissection.

Adults. The specimens observed by T. A. Chapman emerged on March 10, 11 and 12 between six and seven in the morning. The jaws, he says, moved actively and opened so far that they passed one another, the one that had been above sometimes coming to lie below the other. Chapman compares it to the motions of a cabman warming his hands. Having torn open the cocoon and wriggled out of it, the pupa then laboriously digs upward through the earth. The head moves very much, the face is lifted up, and the body is pushed on by the movements of the abdomen helped by its backwardly projecting hairs. At the surface of the ground it lies immovable for some time during which the last acts of transformation take place. Presently the mandibles become immovable even under stimulation, through the withdrawal of the imaginal skin and mandibles together with the strong muscles which remain in the imag-

inal head. The pupal skin now slits open on the median line of the first and second thoracic segments and part of the head. After the usual wriggling movements the adult frees itself from the pupal skin. It expands its wings at once but crawls up hanging them backwards, and very quickly it is in condition for flight.

The flight is described as weak and somewhat irregular. The adults may be taken in the early spring about their host trees. Williams (1908) found a California species (*E. cyanosporsella*) among oak trees at the base of Mt. Tamalpais, by disturbing them from the trunks of the trees early in the morning. "Their flight is rather weak, but hard to follow on account of the small size of the insect. They sometimes feign death, folding their wings like a caddis fly."

At least in the birch forests of Norway, members of this genus have become a considerable pest, though, to be sure, their attack is short-lived.

CHAPTER V

SUBORDER FRENATAE[1]

Leaf-mining larvae occur in some seventeen families of this suborder in our fauna, but in only seven of them (the ones marked with an * below) do they occur in any considerable numbers.

Incurvariidae	Gelechiidae
*Nepticulidae	*Lavernidae
*Tischeridae	Ypnomentidae
*Lyonetidae	Glyphipterygidae
*Gracilaridae	Helodinidae
*Coleophoridae	Tortricidae
Cycnodidae	Pyralidae
Douglassidae	Noctuidae
*Heliozelidae	

The first two of these families include the smallest of the Micro-lepidoptera, and the most primitive members of this suborder.

SUPERFAMILY INCURVARIOIDEA

FAMILY INCURVARIIDAE

There is in this family in America a single well known leaf-mining species, called the maple case-bearer (*Paraclemensia acerifoliella*). It infests the sugar maple, and in the "sugar-bush" of the northeastern United States and adjacent areas of Canada, it is often so abundant as to do serious injury. It has been known since Asa Fitch described it as a leaf-cutter in his first report on New York, Insects (1856). It is

[1] Dr. Martin Hering (1926) states that certain of the European macro-lepidoptera, Zygaenidae and Hesperidae mine leaves. He mentions in particular *Larentia incultaria* H. S. which makes a large blotch mine in the leaves of Primula.

a leaf miner only during its early larval life. Its later surface-feeding habits have been well described by Comstock (1925) as follows:

> The leaves of an infested tree present a strange appearance. They are perforated with numerous elliptical holes and marked by many more or less perfect ring-like patches in which the green matter of the leaf has been destroyed, but each of which incloses an uninjured spot. These injuries are produced as follows. The young larva cuts an oval piece from a leaf, places it over its back and fastens it down with silk around its edges. This serves as a house beneath which it lives. As it grows this house becomes too small for it. It then cuts out a larger piece which it fastens to the outer edges of the smaller one, the larva being between the two. Then it fastens one edge of the case to the leaf by a silken hinge so that it will not fall to the ground "cradle and all" and then turns the case over so that the larger piece is over its back. When it wishes to change its location it thrusts out its head and fore-legs from the case and walks off looking like a tiny turtle. When it wishes to feed it fastens the case to the leaf and, thrusting its head out, eats the fleshy part of the leaf as far as it can reach. This explains the circular form of the patches, the round spot in the middle indicating the position of the case.

Professor Herrick has described its leaf mining and other habits in the paper (1923) from which we have already quoted (p. 48) concerning its egg-laying. We quote now further:

> As soon as the egg hatches, the young larva begins at once to mine in the tissues of the leaf, and it continues to live as a miner for probably about ten days.
>
> In general, the mine is irregularly linear, although it tends to enlarge somewhat toward the terminus and to become a blotch. The mines are most conspicuous from the upper surface of the leaf, and may be very numerous.
>
> The young larva is greenish brown in color, with a dark brown head. The body is somewhat flattened, the prothorax is broad-

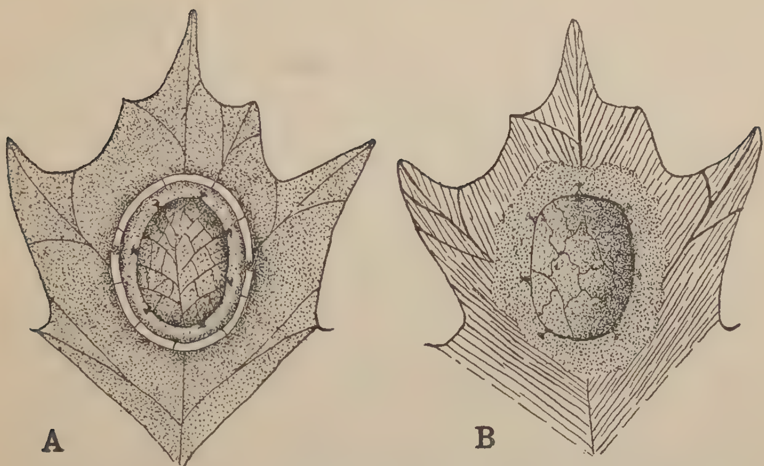


FIG. 30. Two cases of *Praclemensia acerifoliella.* (From Herrick.) *A*, a small case, prepared for enlargement by the cutting of a circle around it; *B*, a mature case.

FIG. 31

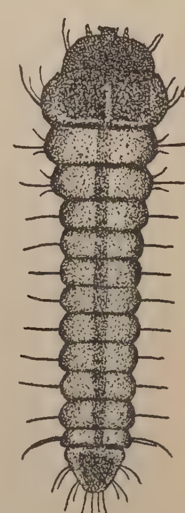


FIG. 29

FIG. 29. The young larva of the maple case-bearer *Paraclemensia acerifoliella.* (From Herrick.)

FIG. 31. Adult moth—maple leaf cutter. (From Herrick.)

ened, and the thoracic legs are present at least during the latter part of the larva's life as a miner. The abdominal segments are prominently enlarged on each side, giving the larva the appearance of a coleopterous larva. When ready to leave its mine the larva is about $1\frac{1}{4}$ mm. in length. The full-grown larva is about [5 mm.] $\frac{1}{5}$ inch in length.

When the larva has completed its growth in the mine, it cuts its oval case out of the mine, apparently always making the lower piece slightly larger than the upper one. It then walks out on the leaf and deftly turns the case over so that the thicker piece from the lower epidermis is on top. The larva grows slowly, occupying all of June and July and part of August to attain its full growth.

The process of cutting and removing a piece of the leaf for enlarging the case is an interesting one. The larva when feeding attaches its case to the leaf by short silken cords at intervals about the edges. Each cord is composed of many threads spun in such a manner that they cross one another near the middle and form an X-shaped cord. When ready to get a new piece for its case, the larva usually cuts a narrow oval slit in the leaf a little distance out from the edge of the case and all of the way around it, so that the piece, when cut, is considerably larger than the case. The new piece, which supports the case with the larva inside, is always held in place while the cutting is going on, by tiny strands of leaf tissue which the caterpillar keeps for supports until it is ready to complete the process. Sometimes the process is varied, the larva cutting a half-oval slit in the leaf extending about halfway around the old case, then cutting a half oval about the opposite end of the case, and joining the ends of the two slits, thus completing the circle. Evidently the larva drags the case to either the upper or the under side of the leaf, as the circumstances require. The position of the case when it is clear of the opening, however, is another matter, for it often requires orientation. If the larva drags its case to the under side of the leaf, the larger piece is on its back, properly oriented; but if the larva crawls to the upper side of the leaf, the larger piece is still on the bottom of the case and the whole case must be turned over, and the larva must also turn over inside of the case. The whole operation of cutting around the case and actually cutting it loose from all support while the larva is

still within seems like a considerable feat—somewhat like sawing off a limb of a tree while seated on it, and yet not getting a tumble.

The cases of the adults vary somewhat in size, but an average specimen has the larger piece on top about 0.4 inch long and 0.3 inch wide.

Thus it would appear that the larva lives as a miner within the leaf during its first stage only, beginning its operations during the month of May. Then it is a surface-feeding case-bearer during perhaps four larval stages, extending through the months of July and August and into September. Then it pupates within the case and hibernates in the same among the fallen leaves on the ground beneath the trees. Then it emerges in late Spring as a moth having a wing expanse of half an inch, and a color of brilliant steel blue with violet reflections, and a tuft of orange-yellow hairs upon the head.

Of this family Europe has more representatives than we, and especially more species that are miners in early life, but with only a few exceptions (as *Incurvaria capitella* which continues to burrow in Ribes stems) they become case bearers in late larval life. Adela and Nematois burrow in flowerheads or seed capsules at first, but Phylloporia, Nemophora and at least some species of incurvaria begin life as miners.

Phylloporia bistrigella of Europe mines in Birch leaves. The mine usually begins near the tip of the leaf as a narrow gallery. Proceeding more or less directly along the midrib it grows slightly wider and near the base it turns up along the leaf margin where it expands somewhat abruptly into a blotch. When the larva is full-fed it cuts oval pieces from the floor and ceiling of the newest made part of the mine and sews them together as a case.

In this it descends to the ground for pupation. Mining is done in July and August and the adult emerges the following June. Nemophora begins as a leaf-miner but

becomes a case-bearer much earlier in life than Phylloporia. *Nemophora swammerdamella* of Europe mines in the leaves of Oak and Beech as a young larva. In late larval life its case will be found to be compounded of several pieces on account of necessary enlargements from time to time as the larva grows.

The known European larvae of Incurvaria are at first either borers in young shoots (*I. pubicornis, I. capitella, I. morosa*) or burrowers in buds (*I. redimitella, I. rubiella*) or, more commonly, miners in leaves. The former habits may have been derived from the latter. Adults emerging very early may have come too soon for leaves, and may have adapted themselves to other succulent parts. The miners feed, some on Oak and Birch and some on members of the rose family; the borers and burrowers seem all to be attached to the Rose Family. Early in life (except *I. capitella*) they one and all begin to wear a case; the miners cutting case from the leaf as do Phylloporia and Nemophora. In their cases they travel about on their host plant or the ground, eating living or dead leaves. When their first case is outgrown, they meet the emergency by fastening one side of their bivalve case to a leaf and cutting out a piece which is shaped like the first but bigger. Then they turn the case over and do as much for the other side. When the larvae are full-fed, their cases will be found to consist of two valves made of several discs of leaf arranged concentricly, with the smallest next to the larva. From these cases the larvae feed from the end of the mining period in late June until they pupate in September or October.

CHAPTER VI

Superfamily Nepticuloidea

FAMILY NEPTICULIDAE

Almost any thicket or fence-row will yield a supply of Nepticulid mines and we have very many common North American species. Nearly all of them belong in the genus Nepticula, which seems to have an almost unlimited number of species. In a comprehensive paper on the American species of this family, Miss Braun (1917) lists some fifty-four species known in the adult state. Many of these she herself has reared; a large proportion of the others have been reared either by Dr. Brackenridge Clemens, or by V. T. Chambers. Continued life-history work will doubtless reveal a large number of additional species within our boundaries.

With the exception of some gall-making species of Ectodemia all the known larvae of this family are miners in leaves or, more rarely, in fruit and bark. In most cases their host plants are deciduous shrubs and trees though some occur on herbaceous plants.

The egg. The minute oval eggs are sealed upon the surface of the leaves with specks of cement which show as minute glistening dots even to the naked eye. The larvae eat their way from the eggs directly into the leaf tissue. It has been observed by Sich that the larva of a European species, *N. acetosae,* takes two hours to get its head half way into the leaf, nearly six hours to get head and thorax in, and twelve hours to get completely in and assume its regular mining position with the venter uppermost. By sectioning mined leaves Miss Braun has ascertained that the larvae

at first confine their feeding to the single layer of palisade tissue next the cuticle. As they become larger a part of the spongy parenchyma also is consumed.

The larva. The larvae are slightly flattened with the head deeply retracted into the thorax. Jointed thoracic legs and crochets are wanting and locomotor appendages are represented only by roughened protuberances. Such projections are to be found in pairs on the second and third thoracic segments and on the second to seventh abdominal ones. Some species are said to have one or two additional pairs.

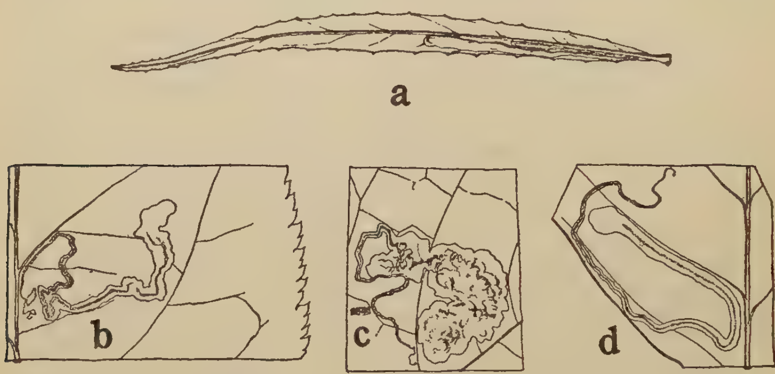


FIG. 32. Typical mines of Nepticula. (From Miss Braun.) *a*, *N. pallida; b, N. pomivorella; c, N. nyassaefoliella; d, N. saginella.*

Miss Braun has ascertained that there are four larval instars and has made some observations on the relative amount of feeding in the various stages. The mine formed in the first instar rarely exceeds a few millimeters in length while the area mined in the last instar is usually much more than half the total area of the mine. She found that the larva of *Glaucolepis saccharella* remained in the mine more than sixteen days. In this species second and third moulting periods each took from thirty-six to forty-eight hours.

The mines as a rule are linear and serpentine but with the very many species of Nepticula comes considerable diversity.

Some become blotched after the larva has reached the third and last instar; some few are blotched from the beginning. The earliest part of the mine is often so small as to be difficult to follow, save perhaps the faint line of excrement that leads back and back and even into the withered bit of egg covering on the surface of the leaf.

The pupa. When the larva is full-fed it cuts a semicircular slit in the epidermis and crawls out of the mine. In rubbish or in surface soil it spins a characteristic cocoon. This may be of whitish, yellowish, brownish, or greenish silk according to the species. Traegardh has pointed out that the cocoons of some, and probably of all, Nepticulids have a very novel and interesting device for enabling the moths to gain their freedom. The silk of the cocoons is firm and tough, and the pupae are delicately chitinized and have no cutting or tearing structures about the head region. That these thin, frail, pupal shells are extruded from the cocoons for the release of the adults depends largely on this peculiarity of the cocoons, namely, that there is a narrow fissure at the anterior end. The edges or lips of this mouth-like opening press firmly together and are forced apart only by the movements associated with the emergence of the adult. Sometimes the borders of the fissure form a projecting rim which may be continued around the entire length of the cocoon. The fissure itself, however, extends only from the anterior end a third of the length down either side and is so inconspicuous that it is not surprising the ingenious arrangement should have escaped the notice of many naturalists.

The pupae are, as we have said, very delicately chitinized. On the back of the abdomen are patches of small setulae which function in helping the pupal shell to pass out of the cocoon. The appendages are free and segmented. Abdominal segments one to seven are apparently free and mobile. The pupal form is flattened and ovate. In the

summer generation pupation takes place a few days before the emergence of the adult. In the hibernating generation pupation may be delayed until spring.

The adult. The moths are among the smallest of all the lepidoptera, some of them expanding scarcely 3 mm. ($\frac{1}{8}$ inch). The two pairs of wings are similar in shape, elongate, ovate and pointed. Some of the species are dull brownish or drab, while others are ornamented with shining metallic spots or bars. They are of a retiring habit and are not often met on the wing.

Typical of this great genus of micros is the plum leaf-miner *N. slingerlandella*.[1] Crosby (1911) has written the best account of the habits of this species, and from his bulletin we quote the following:

> The plum leaf-miner is a new fruit pest and is doubtless a native American insect. The larva first eats a narrow linear mine an inch or less in length, then widens the mine so as to produce an irregular, more or less ovate blotch about one-half inch long. The part of the leaf so injured turns brownish and dies. From three to twelve mines are often found in a single leaf. The trees become partially defoliated and the fruit may fall prematurely.
>
> The eggs are attached to the under surface of the leaf, usually at the forks of the more prominent veins. The egg is about 0.3 mm. long by 0.2 mm. wide, oval in outline, flattened where attached to the leaf and dome-shaped in profile. The green of the leaf shows through the transparent eggshell, making it a difficult object to find. The eggs are most easily located by holding a leaf at an angle in the sun so that the light will strike it obliquely, when they will be seen as minute glistening dots.
>
> In hatching, the larva eats its way out of the eggshell on the underside next to the leaf, and enters the leaf directly without coming out on the surface. This is a point of great practical importance, as showing the futility of attempting to kill the larvae with an arsenical spray. When full grown the larva is about one

[1] Named in honor of the late Professor Mark Vernon Slingerland, who first studied it in New York State.

FIG. 33

FIG. 34

FIG. 35

FIG. 33. The plum leaf-miner—*Nepticula slingerlandella*, adult.
FIG. 34. Egg of the plum leaf-miner, greatly enlarged.
FIG. 35. Grown larva of the plum leaf-miner.

sixth inch in length, greenish white in color with the head light brown; the contents of the alimentary canal show through the semitransparent body wall as a greenish or brownish stripe.

After entering the leaf the young larva eats out a narrow linear burrow, or mine, an inch or less in length, leaving the outer layers of the leaf intact. This part of the mine usually follows a tortuous course but may be nearly straight. The larva next enlarges its mine into an irregular ovate blotch about one half inch in length. In the linear part of the mine the excrement is left as a blackish streak extending along the center of the burrow; in the blotch mine it forms a broad, irregular band along the center, but does not extend to the tip. The outer leaf layers overlying the mines turn brownish or yellowish; the upper layer seems to be thinner than the lower, and the mines are more conspicuous when viewed from above. There are often ten or a dozen mines in a single leaf (pl. 1, fig. 3).

When full grown the larva leaves the mine through a cut in the upper surface of the leaf, falls to the ground, and there constructs a small flattened brownish cocoon in cracks in the soil, under loose stones, or between the base of the tree and the surrounding soil. Where the ground is undisturbed, the cocoons are rarely found more than an inch below the surface. Sod furnishes ideal winter quarters for the cocoons.

The adult of the plum leaf-miner is a small bronzy black moth having an expanse of $\frac{1}{7}$ to $\frac{1}{5}$ inch. The forewings are crossed by a shining white band on the outer third, and the head bears a conspicuous orange tuft.

The work of an apple- and pear-leaf infesting species, *N. pomivorella*, is thus described in Slingerland and Crosby's *Manual of Fruit Insects*, page 74:

The tiny, dark, emerald-green caterpillars, about $\frac{1}{10}$ inch long, make narrow, tortuous or serpentine mines, often 2 inches in length and less than $\frac{1}{16}$ inch wide just beneath the upper surface of the leaves of the apple and pear. The first half or two-thirds of the mine is broader and nearly filled with a continuous zigzagging thread of black excrement. The insect is quite common in

Canada and the northeastern United States. In October, the tiny green caterpillars are sometimes seen hanging by silken threads from the leaves. They soon find their way to the twigs, where they spin small, oval, dense, brown cocoons about $\frac{1}{8}$ inch long on the bark, often in a crotch. These cocoons resemble, and could be easily mistaken for, Lecanium scales. In May the caterpillars transform through brilliant green pupae to the minute, shining, purplish-black moths with tufted, reddish-yellow head, that emerge early in June. Thus far no very serious injury has has been recorded.

CHAPTER VII

uperfamily Tineoidea

FAMILY TISCHERIIADE

The single genus, Tischeria, occurring in North America north of Florida, is represented by more than a dozen species, whose larvae are all leaf-miners. They make blotch mines, that, in some cases, from a narrow, serpentine beginning, widen abruptly into the crude outline of a trumpet (whence the name, "trumpet leaf-miner" applied to one of the best known of them). There is considerable variety of mining habits among them, as to the part of the tissues of the leaf consumed. All of them hibernate and pupate within their mines, and for the purpose, line the interior of late season mines copiously with silk. The preferred food-plants are oaks and chestnuts, though rose and brambles, apple and pear, and a few compositae are the hostplants of single species.

The best known member of this family is one that is at times a serious pest in apple orchards, *Tischeria malifoliella*, the trumpet leaf-miner. This is a native species that originally fed on wild hawthorns and crab-apples. It has taken kindly to the cultivated apple. It has more than one brood per season (two at Ithaca and four at Washington, D. C.) and the later broods may infest the leaves so heavily as to cause the foliage to wither and drop several weeks earlier than it should, thus preventing the proper maturing of the fruit, and weakening the tree.

The moth has an expanse of wing of about a quarter of an inch (6 mm.). It is gray in color, tinged with purplish, "the scaletips showing some golden iridescence."

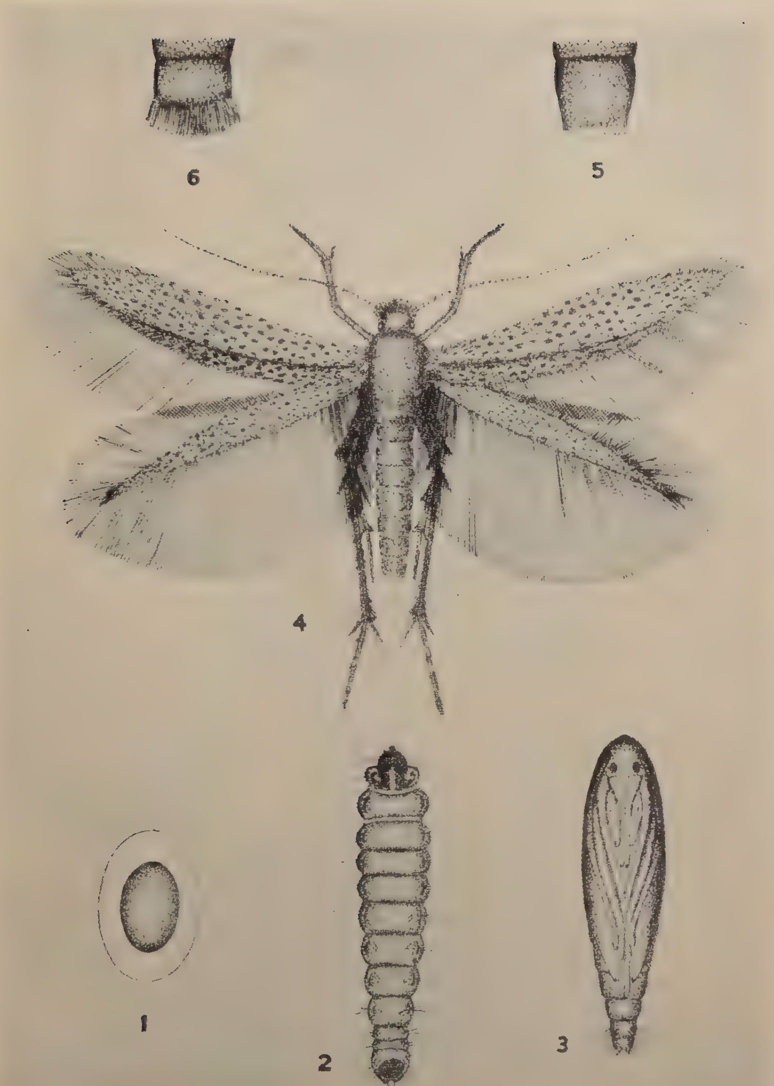


FIG. 36. The trumpet leaf-miner of the apple *Tischeria malifoliella*. *1*, egg; *2*, larvae; *3*, pupa; *4*, adult. (After Dunnam)

The mines are more or less trumpet shaped, as the common name implies, though the blotch portion is often oval or irregular, and the basal half is often marked with transverse crescents of white (due to intervening depositions of dark colored frass), making them easily recognizable (see pl. 2, figs. 2 and 3). They occur on the upper surface, involving the palisade layer of leaf parenchyma. Generally they do not cross the larger veins.

The best description of the immature stages is that of Quaintance (1907), from which we quote as follows:

The egg. The eggs of *Tischeria malifoliella* are regularly elliptical in outline, somewhat convex centrally, but flattened around the margin, which area is more or less wrinkled. When first laid they are greenish yellow in color and somewhat translucent. In some lights they are irridescent, as are the empty egg shells. One or two days previous to hatching they become comparatively conspicuous, the embryo being central and the whitish margin showing plainly against the dark color of the leaf. The empty shells are white and mark the beginning of the mine. The eggs are attached closely to the leaf, usually in furrows along a veinlet, but occur more or less promiscuously.

The larva. The larva upon hatching measures about 0.7 mm. in length. The head is brownish, the rest of the body whitish, except cervical and anal shields, which are dusky. Full-grown larvae will average 5 mm. in length by 1 mm. in width across the third thoracic segment. The head is about 0.5 mm. wide, retractile, bilobed, brownish or even black in color. The general color of the body is light green, except cervical and anal shields, which are brownish. The body is flat, with the segments very distinct, and tapering caudad from the second or third segment, the last three segments rounder and narrower then the preceding. Thoracic segments with three long setae on each side; succeeding segments with two setae on each side varying considerably in length; at caudal end there are numerous shorter curved setae. Thoracic legs absent. Abdominal and anal legs marked by five pairs of crochets.

The pupa. The pupa is rather variable in size, the average of five being 3.35 mm. by 0.95 mm. The color when first formed is rather uniformly pea green, later becoming much darker, varying with age. The general color of the thoracic region and head is dark brown to blackish. The abdomen is dark green, yellowish caudad; the caudal margin of the rather distinct segments is brown. Leg and wing sheaths free.

In the vicinity of Washington the mid-summer generation has a life cycle of about 33 days.

FAMILY LYONETIDAE

In this family are included a number of minute moths, having many structural characters in common, but having larvae whose form and habits fall into three principal groups, as follows:

I. The *Lyonetia group,* whose tissue feeding larvae are miners through life, but pupate outside the mine, generally attached beneath a leaf under more or less protection of spun silk. The mines are first serpentine and then blotched, and are usually filled with scattered blackish frass.

II. The *Phyllocnistis group,* whose legless, sap-feeding larvae shear through the palisade cells of the leaf during four feeding stages; then, becoming more cylindrical in form, rest in a chamber formed in the leaf at the end of the mine, during a final larval stage, and then pupate in the same chamber. The mine is narrowly serpentine throughout, and is of the almost invisible "snail trace" type, with hardly more than a central tracing of frass.

III. The *Bucculatrix group,* whose ordinary tissue-feeding larvae are equipped with good thoracic legs, and make small serpentine mines during the first stage only, feeding thereafter openly from the surface of the leaf.

Group I

Of the first group of the Lyonetidae we have in North America representatives of four well-known genera, Lyon-

etia, Leucoptera, Proleucoptera and Bedellia. The mines of most species of this family are at first narrow and linear. That of *Lyonetia clerckella,* Clerck's Apple Miner of Europe, continues to be linear until the end, but most species in late larval life expand their mines into blotches. A few make blotch mines even at the beginning. The larvae consume nearly all the tissue between the upper and lower cuticles including much of the fibrovascular system. The amount of frass is very large and it accumulates in the mines of most of the species, making them appear as blackish or brownish lines or spots. Some of the species take pains to avoid contact with their frass by extruding it through holes in the cuticle and the mines of such species are clean and transparent.

The eggs of most species, so far as known, are said to be laid on the surface of the leaves of the host plants.

In form the larvae are less depressed than are many of the lepidopterous larvae whose whole feeding period is spent in the mine. In *Bedellia somnulentella* and *Proleucoptera smilaciella,* at least, the front does not reach the vertical triangle and the body is cylindrical with moderate incisions. In these species the ocelli have a rather peculiar arrangement, for the first and second are nearly contiguous and the second, third and sixth form a vertical row in front of the fifth. The thoracic legs are present and segmented and a complete uniserial circle of uniordinal crochets is borne by the prolegs of segments 3, 4, 5, and 6 of the abdomen. *Leucoptera spartifoliella* of Europe differs from the American species in that the front does reach the vertical angle and that the crochets of the ventral prolegs are in a double instead of a single row in the caudal half of the circles (Fracker, 1913). Some species are said to use lateral mammillations of the segments as organs of progression as do Phyllocnistis larvae.

The pupae of the Lyonetiidae represent a transition stage

between the condition in which some segments remain unfused and mobile, and that in which the outside covering of the pupa is entirely fused and soldered; for though they are immobile, and though the appendages are attached to the body wall and the segments are attached together, the fusion is incomplete and soldering weak and the parts may be split from one another more easily than in most immobile pupae. They possess neither backwardly pointing spines on the dorsum of the abdomen nor cutting edges on the cephalic extremity. Such structures are to be associated with mobility in the pupae and emergance of the pupal shell before the release of the adult. The pupae of Leucoptera and Proleucoptera are shorter and thicker than are those of Bedellia and Lyonetia. Bedellia pupae have a long cephalic projection and well-developed ridges and projections on the body.

Pupation always takes place outside the leaf in this group. In other respects the members are not very uniform in pupating habits. Some make cocoons and some make none. The naked chrysalis of *Bedellia somnulentella* is held horizontally against the under surface of the leaves, supported by recurved spines upon crossing threads. *Lyonetia latistrigella* pupa is likewise naked and this is suspended by means of a few silken threads across a bent leaf. Some species prepare a delicate web on the underside of the leaf which has the form of a letter H with a very broad cross bar. Between this broad median band and the leaf surface some species, as *Leucoptera coffeella*, transform to pupae without forming any definite additional cocoon. Other species spin cocoons between such a web and the leaf. In *Leucoptera pachystimella* and *Leucoptera albella* the cocoons proper are supported against the leaves or other surfaces by short bands or cables. *Lyonetia clerckella* of Europe and our native *Lyonetia speculella* spin cocoons which are slung hammock-wise by the extremities of the cocoons themselves upon the lower surface of slightly curved leaves.

There may be from two to several generations a year in this family. Though our native species are not known to have economic importance, *Lyonetia clerckella* and *Leucoptera scitella* are well known minor pests of fruit in Europe and *Leucoptera laburnella* disfigures plantings of laburnum and lilac there. *Leucoptera coffeella* which is known to attack coffee almost everywhere that it is cultivated comes near our borders in the West Indian plantations.

Of the type genus Lyonetia we have in North America several species whose mines are also known. Miss Braun has recently reared two nearly related species from Rhododendrons, one of which she described under the name *Lyonetia candida*. The other rhododendron species, *Lyonetia latistrigella,* was bred from mines in young tender leaves of the Great laurel, *Rhododendron maximum,* at Balsam, N. C. The first three centimeters of the mine appeared as a very fine black line, for three more centimeters it widened somewhat though still being distinctly linear and then expanded into an elongate brownish blotch some 4 cm. long and about 5 mm. wide. As has been said, the naked chrysalis is suspended by means of a few silken threads stretched across a bent leaf. *Lyonetia candida* was reared from mines in *rhododendron occidentale* in California and from *Rhododendron albiflorum* in Washington. Its mine is said to be very narrow and linear for from 3 to 4.5 cm. and then to enlarge abruptly into an irregular blotch. The pupa is enclosed in a slight white cocoon. *Lyonetia saliciella* was also reared by Dyar in British Columbia. It lives in the leaves of willows making mines similar to those of *L. speculella. Lyonetia alniella* is said to make large brownish blotch mines in leaves of alder in the northeastern United States.

Frost (1924) has studied the habits of *Lyonetia speculella* which mines the leaves of apple and other hosts. The larvae make short linear mines which later broaden into blotches obliterating the original linear portion. Several

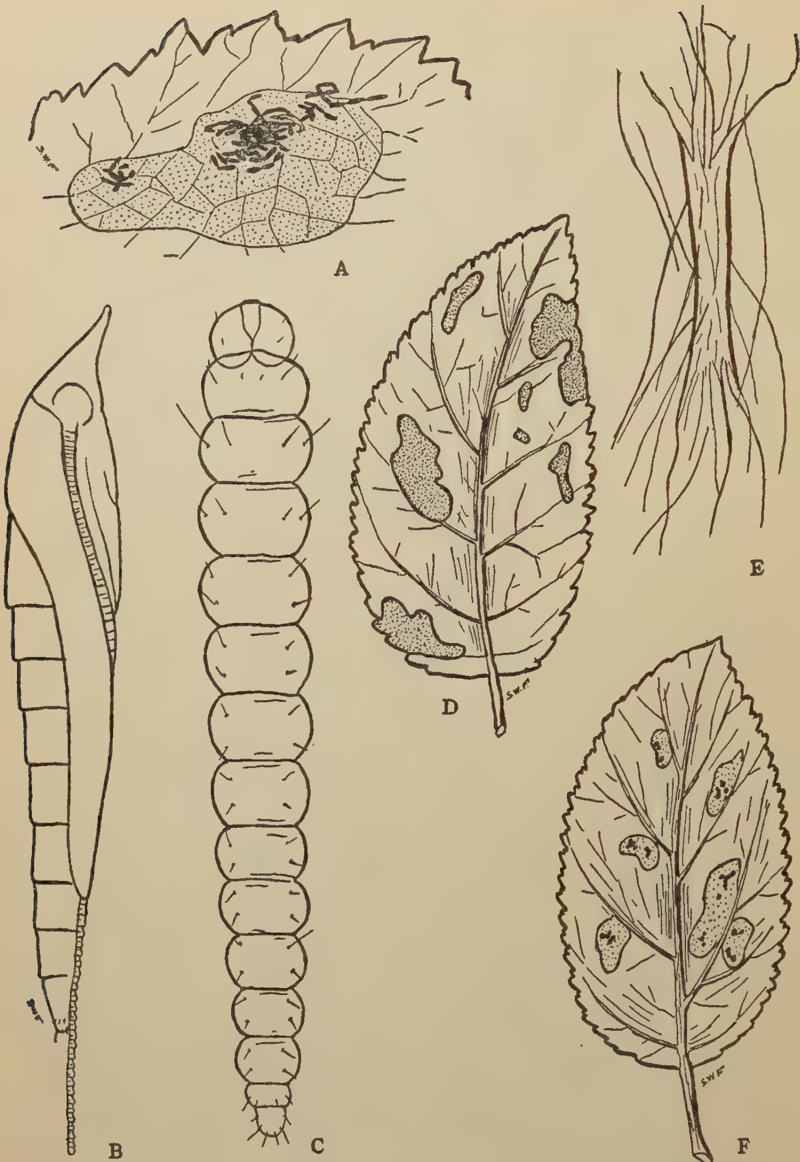


Fig. 37. The apple leaf-miner, *Lyonetia speculella*. *A*, a bit of an apple leaf showing frass extruded from holes in the mine; *B*, pupa; *C*, larva; *D*, upper side of leaf showing mines; *E*, cocoon, *F*, lower side of apple leaf showing appearance of mines. Drawn by S. W. Frost.

mines may be found on a single leaf. They occur on the upper surface and are slightly visible from the lower surface of the leaf. A small amount of frass is scattered in the linear portion of the mine but later as the mine increases in size it is ejected through small holes cut by the larva through the lower epidermis of the leaf. As the frass is pushed from the mine the pellets adhere end to end presenting a linked appearance. Later the frass becomes massed about the opening through which it was pushed.

The larva is cream in color and distinctly constricted between the segments, giving it a bead-like appearance. Thoracic legs are present, the prolegs are rudimentary and represented on the third, fourth, fifth and sixth segments by uniserial circles of crochets.

The full-grown larvae abandon the mine and pupate in a delicate white silken cocoon somewhat tubular in shape and fastened by means of a few silken threads to the under surface of the leaf which is often curled for protection. The pupa is light brown in color with the antennal sheaths projecting greatly beyond the tip of the abdomen and with the head produced into two distinct points.

Bedellia somnulentella is found both in Europe and in America. It was first described in Europe but as its favorite host, the morning glory (*Ipomoea purpurea*), is a native of American tropics this may also have been native to America. Clemens first called attention to the insect on this continent and gave a good account of its habits. When young the larvae make narrow transparent mines, marked with a central line of frass, in the leaves of the morning glory. When partly grown they desert these initial mines and, half-looping over the leaves, enter between the cuticles at a new place. From that time until they are full-fed they eat out the parenchyma in blotches, making one or more blotch mines. During this part of the feeding the larvae either leave the anal segments extruded through the

entrance hole or they return to it to eject excrement. In passing over the leaves they hold to the surface by threads which they spin on the leaves about the mined area. In changing to a pupa they attach themselves by their anal extremities to a junction of such threads and are held in a more or less horizontal position upon other cross threads by dorsal recurved bristles. The adult is a yellow moth having a wing expanse of two-fifths of an inch.

Leucoptera and Proleucoptera are closely related genera. The first species of this group to be reared in this country was probably *Leucoptera albella.* It attacks several species of poplars and willows and has a wide distribution. Chambers reared it in the Ohio valley. Dyar found it attacking particularly the narrow-leaved cottonwood, *Populus angustifolia,* in Colorado. The mines are large black blotches frequently involving the whole leaf. The larvae are gregarious, a single leaf and mine being shared by several individuals. The abundant black frass is contained in the mines. It appears that there are at least two generations a year. The larvae being abundant in June and again in September in the transition zone. When they are full-fed the larvae emerge from the leaves and on the lower surface spin bands or cables of purest white silk. They then make flat, oval, white cocoons between the cables and the leaf surface and transform to pupae. *Leucoptera pachystimella* attacks the old leaves of the evergreen plant, *Pachystima myrsinites,* in western North America. The mines are at first linear and follow the margin but later they expand into a blotch which involves the whole of the surface of the small leaves. The frass is contained in the leaf but is packed rather firmly into one end of the mine. The cocoon of this species, like that of the preceding, is spun between bands of silk and the lower surface of the leaf.

Proleucoptera smilaciella as an adult is an exquisite little moth, clad in ermine and decorated with gold and silver and

jet. The antennae and legs are white, with a golden sheen. The thorax and fore wings are white and the hind wings are blackish; the fore wings are marked with a golden streak and golden spot, both narrowly edged with black; also, with a black spot. And the white fringing marginal scales are black-tipped. Other scales on the wings are tipped with silver and bronze. The wing expanse is about a third of an inch.

We quote Busck's account of the habits of the species, as follows:

Food-plant: *Smilax glauca*, and *S. rotundifolia.*

The eggs, which are laid on the underside of a leaf singly, but often 2 to 5 on one leaf, are oval, glistening white and very large in proportion to the moth.

The young larva eats into the leaf, forming a short, narrow, serpentine track, which soon broadens out in a large irregular upper blotch mine, often entirely obliterating the early part of the mine. The mines show reddish brown on the upper side of the leaf and contrast very conspicuously with the dark-green foliage. The black frass is distributed irregularly in the mine, the inside of which is a dirty domicile for such a dainty creature to issue from. The larva is, when full grown, 5.5 mm. long moniliform, somewhat flattened and tapering backwards; first thoracic segments the broadest, nearly twice as wide as the head. Head light brown, body dark, glossy-greenish with two longitudinal black spots on first thoracic segment; and legs normal. Often two to five larvae are found within a common large mine.

When fully grown the larva quits the mine through a moon-shaped cut in the upper epidermis and spins a beautiful glistening white bridgework, consisting of two paralel broad flat silken bands each about 10 mm. long and 1.5 mm. wide, connected at the middle, under which the spindle-shaped snow-white cocoon proper is made.

Several overlapping generations are found during the summer in this locality, the moth issuing from the middle of June to late in September. The insect over-winters as imago.

Group II. Phyllocnistis

The young larvae of Phyllocnistis are so flat they look as if they had been run over by a steam roller. They are exclusively sap feeders, having flat triangular heads, thin cell-shearing mandibles (see fig. 22), and a series of lateral expansions of body segments into paired marginal lobes giving a moniliform outline. They are quite destitute of legs.

The mines are very long, narrow and tortuous. Their shape perhaps has some relation to the complete repression of the usual motile organs and the use of the very elongated lateral mamillations in progression. Since the larvae do not ingest any of the solid matter of the leaf, the mines are but slightly transparent, even in thin leaves, and in the thicker ones do not show at all by transmitted light. By reflected light the mines show as white tracings on the leaves. In some cases there is a central frass line of a dark color, for instance in the mine of *P. populiella;* in others one cannot distinguish any sign of excrement as is in the mine of *P. vitigenella* in grape. The course looks like a tiny tracing of mucous substance on the surface—a "snail's track" it has been called.

In the fourth instar the larva assumes a strange form. It is more nearly cylindrical than in the earlier instars but of the mouth parts only the spinneret is functional. The mandibles are rudimentary. Eyes are lacking entirely. At the end of the third instar the mine is slightly widened and in the pocket thus formed the fourth instar begins. The larvae employ the newly developed spinneret in spinning silk over the entire inner surface of this expansion. The thin cuticle shrinks as the silk dries and, as the pocket is usually formed at the very edge of the leaf, this causes the margin of the leaf to be folded over the larvae in a little pucker or knot. More silk is spun within to make the walls firm and then the larvae transform to pupae. In less than

two weeks in summer the pupal shells are thrust through the cocoon walls and there emerge the daintiest of shining or silvery white moths with smooth rather than with tufted heads.

These larvae seem to disturb the metabolism of their host plants to a very slight extent and the only species which has received any attention from economic workers is *P. citronella*, which mines the leaves of citrus fruits and is particularly abundant in India and Ceylon. It is reported

Fig. 38. The mine of *Phyllocnistis* on poplar leaf. Note the "nidus" at the end of the mine.

to have been introduced into the United States on nursery stock but so far has not become generally distributed.

P. vitigenella which mines in cultivated grapes is a species whose mine is particularly like a snail's track. One needs to see the little yellowish larvae working away under the cuticle to be persuaded that these are indeed mines. These larvae usually form their pupating chambers at the leaf's edge, but in large leaves they may spin under the cuticle an inch or more from the border.

P. populiella is one of the commonest of the species of

this genus. Its mines on the upper side of the leaves of poplar are quite characteristic and conspicuous. The separated epidermis is in a wider tract than in the other species I have seen. It is shining white—by reason of the film of air separating it from the parenchyma—except in a narrow stripe at the center where it adheres again on account of the dark-colored semi-fluid excrement which is deposited there.

Group III. Bucculatrix. The ribbed-cocoon makers

Mining operations of this genus are, for the most part, confined to the very young larvae, which make narrow, brown, gradually widening serpentine mines, and later emerge and feed externally on the surface of the leaf. In this they are unique among lepidopterous larvae. One of our species, *Bucculatrix crescentella,* recently described by Miss Braun, is said to do no external feeding but to emerge from the mine when full-fed and to spin at once the usual type of ribbed cocoon. On the other hand some species—perhaps through lack of observation—are not definitely known to be miners at all. Most species feed between the cuticles of the leaves of their host plants until about the end of the first instar. *Bucculatrix ambrosiaefoliella* is said by Chambers to moult once in the leaf and once under a moulting cocoon on the leaf before spinning the pupating cocoon. *Bucculatrix pomifoliella* and *B. thurberiella* emerge from the leaf before the first moult and undergo two moults in moulting cocoons.

The egg. The eggs of a few species have been observed. All are deposited upon the leaves but from the available descriptions they seem to bear little resemblance to one another in form. Chambers describes the egg of *B. ambrosiaefolia* as a "minute colorless globule." Those of *B. pomifoliella* are scattered on the under surface of the leaves of apple and are said to be "minute, pale green, elliptical, iridescent and roughened." Those of *B. thurberiella* were

found on the upper and lower surfaces of the leaves of cotton. They are described as very small, barely discernable to the naked eye, and pale straw-colored with a reticulate system of smoky mottlings. They are projectile-shaped with about ten longitudinal ridges and intervening grooves and are placed upright on their larger ends.

The larva. The larvae as a rule bore directly into the leaf tissue at the point of attachment of the egg. They move to the upper layer of the parenchyma and there tunnel out narrow serpentine channels. In form they are more or less cylindrical, tapering slightly toward the head and tail, with moderate intersegmental incisions. The head is not particularly elongate or flattened. The front extends about two-thirds of the way to the vertex while the adfrontal pieces reach it. The thoracic legs are present and segmented. The prolegs which occur on segments 3, 4, 5, 6 and 10 of the abdomen are slender and rather long. The well-developed uniordinal crochets are in two transverse bands on the ventral prolegs and in single transverse rows on the anal ones. While they continue to mine the larvae are smooth but when they become external feeders they are rough as though shagreened and are possessed of wart-like tubercles, bearing hairs.

When the larvae emerge and feed on the outside of the leaves they skeletonize them. Eating away one cuticle and most of the soft interior tissue, they leave the other cuticle and the fibrovascular system intact. Before each moult that they undergo on the outside of the leaves, they spin special moulting cocoons (see pl. 1, fig. 2). When there are two external moults the second cocoon slightly exceeds the first in diameter. They have the form of more or less circular, flat webs spun upon the leaves somewhat less in diameter than the larvae are in length. The larvae therefore assume a curled or looped position beneath them. In about a day after retiring below them the larvae emerge

again and feed in the following instar in an entirely similar way.

When the larvae are full-fed they spin pupating cocoons. These are sometimes placed on the leaves themselves, but are more often to be found on the twigs or upon nearby herbage. Save in a few species that feed on compositae, they are elongate structures of a workmanship so delicate and finished that they have been the wonder and admiration of naturalists of many generations. Because they are so remarkable in themselves as well as being so characteristic of the genus, we use the name, the ribbed-cocoon maker (first suggested by Slingerland for the common species on apple) to apply to any member of the group. A careful and appreciative account of the making of such a cocoon was written by Charles De Geer before the middle of the eighteenth century. It will be found in the first volume of his *Memoires* under the heading "Little, green, naked caterpillar with sixteen legs which gnaws the lower surface of the leaves of the frangula and is nourished of them." Though the account is long it seems to me to warrant extensive quotation.[1] He says

> When they [i.e., the larvae] have attained their full size . . . . they spin upon the leaves extremely pretty little elongate cocoons, that are noteworthy because of their unusual form. . . .
>
> They are of about the same length as the caterpillars. Their color is greenish white . . . They are marked longitudinally with folds. . . . which show on the cocoon as rather deep furrows. One may count seven, eight or nine of them on each cocoon and they extend from one end to the other. . . . The form [i.e., of the cocoon] is like the half of a very elongate spheroid that has been cut in two along its greatest diameter; for the lower side of the cocoon, the surface which is applied to the leaf, is flat and smooth and the other or superior surface is convex.
>
> The ridges and the furrows of the cocoon indicate much industry

[1] The translation is by Mrs. Tothill.

on the part of the little caterpillar that is the maker of it and one would not be able to imagine how it could have made them. This the caterpillar must teach us, and it is only by discovering it in the labor itself that one can understand how it succeeds in spinning so pretty a cocoon. I have been fortunate enough to observe one of these caterpillars at the time when it began to work at the construction of its cocoon and I am going to make known that which it made me see, as clearly as I possibly can and in as much as the very small size would allow.

I will remark first of all, and it is a thing worthy of attention and uncommon, that until the caterpillar had completed a half of the cocoon it remained entirely outside of it. We know that ordinarily caterpillars enclose themselves in the cocoons at the same time that they work at them, that in proportion to the progress of the construction of the cocoon the body of the caterpillar becomes more and more covered. But our little caterpillar proceeds quite otherwise. It lays first, so to speak, the foundation of one of the ends of the cocoon that it intends to spin, it adds new threads to this little beginning, and other sets of threads to these and so on. As the work advances the caterpillar moves backward, and its body remains nearly in a line with the cocoon and entirely outside of it. It touches only with the head and the horny legs the edge of the cocoon.

When half of the cocoon, or to speak more correctly, half of the outside layer, is completed, the caterpillar stays its work for some moments. We notice that it then enters head first into this half-cocoon. It next turns around in it by doubling its body. . . Finally it comes into a reversed position so that then the posterior part is found in the small or pointed end. . . . of the started cocoon and the head and the anterior part of the body is outside of the half-cocoon.

Next it begins to work at the other half of its cocoon. At a distance from the edge of the half-cocoon about equal in length to this same, it begins to spin the pointed end of the other half; the length of the body serves it as a measure for not beginning this half at too great a distance away. It spins this new portion in the same manner as the first. As the work advances it draws the head back; but as the posterior part of the body is in the finished

half of the cocoon it cannot retreat any further and instead it contracts the body more and more. . . . But when the new portion of the cocoon is so advanced that the body can undergo no more contraction for applying the head to its edge then it bends the fore part of the body considerably. It turns the head back over the body and so is still in a position to apply the spinneret to the border of the cocoon. . . . When the distance between the edges of the two halves of the cocoon becomes very small there is only room for the head between them, and at last this distance diminishes to such an extent that there is no longer room for the head to move without disarranging the tissue of the edges. The caterpillar was then obliged to close this opening in another way. . . . It changed entirely its manner of working. It drew its head into the cocoon and then stretched threads of silk between the two edges parellel with the long axis of the cocoon. It added other threads to these and in this manner it soon joined together the edges of the two portions of the cocoon. In all the finished and complete cocoons it is easy to recognize the place where the two parts have been joined together where there is always a little area across the cocoon in which the ridges or cords of the two halves do not exactly correspond, where they do not fall quite in line. . . .

The construction of the tissue itself is noteworthy. When the cocoon is entirely finished it then appears only as a closely woven tissue, marked with longitudinal ridges or cords. . . . But let one examine the cocoon with the aid of a microscope when it is only begun or when only half is done or while it is still not entirely closed, and he will see that the threads attached to one of the ribs pass to the next one and so on. There are two sets of these threads between each pair of ribs and these extend obliquely, but the threads of one set are arranged at an angle to the threads of the other set so that those of the first are crossed by those of the other and thus they form meshes like those of fishing nets. They adhere together in the places where they cross one another. . . . . That the threads are not stretched between the ribs as are the strings on a violin or a harpsicord, but that they are lax and that they have a downward curve and thus together form a little groove between the ribs. . . . . The half cocoon at which the cater-

pillar works is made of but one single continuous thread which it fixes and attaches at various places.

Here follows a detailed description of the method of weaving the net, illustrated by a diagram. Then De Geer continues:

When the two halves of the cocoon have been joined together the caterpillar lines it all over with a good layer of silk which closes all the openings of the meshes formed by the threads between the ribs; so that in the cocoons which are all finished, one can no longer see these meshes so prettily arranged.

The caterpillar at the same time makes a floor for the cocoon. It covers with a layer of silk the part of the leaf on which the cocoon is placed so that it finds itself surrounded on all sides by walls of silk.

Thus wrote this good Swedish observer nearly two centuries ago; and more recently naturalists of our own have, like him, discovered Bucculatrix larvae in the beginning of their labors and have watched the process with eager interest. Though the cocoons of our native species vary in minor points of color, size, number of ribs and the like, the general method of construction is essentially the same. Chambers (1882) described the construction of the cocoon of *Bucculatrix ambrosiaefoliella* as he observed it under the microscope, and he gives a figure to show the way the ribs are built up which is very like that of De Geer. Mr. James Fletcher watched the cocoon of *Bucculatrix canadensisella* from its beginning and described its construction in detail. Slingerland and Fletcher (1903) described and illustrated in fullest detail the cocoons and cocoon making of *Bucculatrix pomifoliella.*

The pupa. The pupae are rather short with a projection in front for piercing the stout cocoons. The appendages are not soldered to the body wall. The abdominal segments 3 to 7 in the male, 3 to 6 in the female, are movable

and the dorsum of the abdomen is provided with backward-pointing bristles. The tenth abdominal segment has prominent lateral projections ending in stout, straight, lateral spines.

At the time of the emergence of the adults the pupal shells are protruded from the cocoons.

The adult. The adults of this genus are wont to have rather decided markings often of brown, black and silvery white. The basal segment of the antennae is extended to form an eye cap. The head is tufted and the face is smooth.

The ribbed-cocoon maker of apple, Bucculatrix pomifoliella, is undoubtedly the one of our species most generally known. This species is distributed very generally in eastern Canada, and in the United States from Maine to Texas. Though usually not a serious pest, it becomes at times locally abundant. Like the cigar case-bearer and the trumpet miner, it seems to prefer the imported and cultivated apple to the native pome fruits with which it originally contented itself.

The adults from hibernating pupae emerge when the apple leaves are unfolding in May in the northern states. They are small (2 to 3 mm. in length), in color light brown and marked on each wing with a dark brown spot. The moths pair about three days after emergence and soon the eggs may be found among the hairs on the lower surface of the leaves, especially towards the center of the leaves.

After six to ten days the tiny caterpillars bore directly through the egg-shells and cuticle and up through the parenchyma to the tissue just below the upper cuticle. For about a week the larvae remain in the leaves tunneling out narrow, brown, gradually widening serpentine mines. When the larvae are 2 to 3 mm. long and the mines about 2 cm. long they cut a slit through the upper cuticle and come out on the leaf. There they soon spin small circular or oval silken webs, their first moulting cocoons. Taking a position on this network the larva bites a small hole near its edge and,

then, as one would turn a somersault, it puts its head into this hole and disappears beneath the silken covering. It dives in, so to speak. It remains in retirement about a day and then having cast its skin, it re-emerges and begins feeding on the surface of the leaf.

In their second instars the larvae bite into the leaf tissue from above and especially towards the borders of the leaves. The feeding scars show as little brown depressions going part way through the leaves. After a few days of feeding the larvae make second moulting cocoons which are slightly larger than the first ones. They again remain in retirement about a day. In their last stage they skeletonize the leaves for about a week.

When full-fed the larvae wander about seeking a place to pupate. Early in July they spin their ribbed cocoons on the leaves, the young fruits, the twigs or the larger limbs. In the transition zone the pupal stage of this generation lasts about two weeks and the next generation of moths is emerging by or before the beginning of August. Farther north there is apparently but one generation of the insect. The species overwinters in the pupal stage. The major part of the cocoons are spun on the lower side of the small twigs especially of the lower limbs.

Bucculatrix thurberiella, the so-called cotton leaf perforator, has recently attracted some attention in the southwest because of its actual and potential economic possibilities. In 1913 it was taken by W. D. Pierce on wild cotton, *Thurberia thespesoides,* at various points in Arizona. Later it was found attacking cultivated cotton in Arizona and in 1916 Mr. E. McGregor found it attacking and doing serious injury to cultivated cotton in the Imperial Valley of California.

In life history it greatly resembles the preceding species. In this case, however, the eggs are scattered on both sides of the leaves and the mines which the young larvae make

are about 2.5 cm. long. Upon emergence they may or may not feed for a short time before spinning their first moulting cocoons. These initial moulting webs are said to be spun on the under sides of the leaf usually over a slight depression; and consist of two fabrics. A somewhat concealed aperture is left through which the individual makes exit after moulting. The webs are about $\frac{1}{16}$ of an inch in diameter. The larvae are in retirement about twenty-four hours.

In the second instar the larvae feed on either the upper or the under surface of the leaves, devouring the tissue only as far as the opposite epidermis. Irregular lesions through the leaves are often formed, when, in drying, the tissue adjacent to these feeding scars collapses. The second moulting cocoons are begun, in southern California, during the second day after the reappearance of the larvae on the leaves. These webs are similar to the primary ones but larger. The larvae spend a little more than a day in retirement before appearing in the leaves in their third instar. After about two days of continued feeding the larvae spin the ribbed pupating cocoons. It is in this third instar that the larvae feed most aggressively and do most serious injury to the cotton.

The pupal cocoons are usually spun upon some part of the plant, sometimes on the leaf blade, often on its petiole, but most frequently at some point along the main or lateral stems. Previous to beginning the cocoon proper the larva spins a series of stout upright bristles in a graceful ellipse around the spot where the cocoon is to be (McGregor). These may have the function of deterring the approach of predaceous enemies.

These species in general illustrate the Bucculatrix habit and by varying details of host plants, color of cocoons and the like, one story might apply to many. Some variations from type have been noted above, namely, Chambers' statement that *B. ambrosiaefoliella*, feeding on ragweed, under-

goes its first moult within the leaf and Miss Braun's statement that *B. crescentella*, which makes trumpet-shaped mines marked with a central line of frass in leaves of various composites, does no external feeding. On the other hand, we lack any definite information that *B. canadensisella*, the birch leaf skeletonizer, is a miner at any stage and this despite repeated notice in connection with conspicuously severe outbreaks in northeastern North America. Probably it resembles related species and mines in the first instar but of the scores who have observed its moulting and pupating cocoons and the effect of its external feeding on the leaves, the late James Fletcher alone makes any statement of observing mines in the leaves. He found small mines which he supposed had been made by the caterpillars in their first stage but he did not actually find larvae of *B. canadensisella* in the mines. Neither he nor any other observer record observation of the eggs. From the time of spinning its first moulting cocoon on the leaves it resembles the ribbed cocoon maker of the apple in habits.

GRACILARIIDAE

This is the great family of leaf-miners. Within it are enrolled about as many species as of all the other lepidopterous miners taken together. In numbers of individuals they are dominant in whatever places of the earth the leaf-mining habit has been particularly observed. The family seems to be cosmopolitan in distribution. The species have been studied particularly in Europe and North America, but there are scattering life-histories published from India, Japan, Hawaii and elsewhere.

Yet despite the countless millions of these little larvae, taking each its tiny portion of the herbage of the world, but few indeed of the species are accounted as pests. Not only does their minute size partially excuse them, but in feeding habits most of them are very precise and economical of

tissues. They take just enough to sustain and mature their own lives, and they injure little tissue save that which they ingest. Even where they are abundant they seem not to injure their hosts very seriously.

Through a greater or less portion of the larval life they are highly specialized sap-feeders, equipped by nature for obtaining the maximum benefit from the leaves with a minimum of injury to them. We have already discussed (p. 56) the two forms of larvae of the different instars of this group and the modifications of mouthparts for cell-shearing and sap-feeding. The first form larva is always the flat, sap-feeding form and the transition to the ordinary, cylindric, tissue-feeding form comes at different instars in the several genera and with varying degrees of completeness.

In the earlier sap-feeding instars the body, head and mouthparts are always very flat. The body is widest in the thoracic region and tapers thence rather rapidly towards the rear end. Each segment, though very thin, pouches out much at either side, leaving very deep lateral incisions between the segments. This distribution of bulk apparently facilitates bending, from side to side without causing a vertical extension of the body.

The legs and prolegs are so much reduced in these instars that at most only the faintest rudiments are discernible. When discoverable prolegs are present they occur only on segments 3, 4, 5 and 10 of the abdomen.

In all the genera of the Gracillariidae there are, according to Chapman (Chambers to the contrary) at least two flat, sapfeeding instars. In the most primitive genera there seem to be five instars in most cases, of which the first two are sap-feeders, while the last three differ very little from unspecialized externally feeding caterpillars. During the latter instar most of them become external though concealed feeders. But in the more specialized genera, Lithocolletis, and its immediate allies, there may be five or seven larval

instars, the first three of which, so far as known are sap-feeding. These relations are indicated in the table on page 61. Certain details of the shift of form will be cited in the account of particular species, such as *Acrocercops strigifinitella* (see p. 124).

The marked change in form between the earlier and later instars is always associated with changes in habits. Most forms become external feeders after this change. Their newly acquired spinning abilities are brought into play in bending the leaf into a roll, or cone, or fold for shelter, and later in spinning cocoons for pupation. Among the Lithocolletis allies there is always a distinct change in habit and this change manifests itself differently in the various genera. In Lithocolletis proper, after the third instar the larvae cease extending the mine and begin going over the area from which the cuticle has been freed, picking out the parencyhma. They use their spinning abilities in causing the flat mine to become tentiform by spinning silk across the loosened cuticle, and drawing it into folds. The Lithocolletis larvae of the flat type (the Cameraria group), which only in part resume the cylindric form after the third moult, continue to extend the borders of their mines during two additional feeding instars, and then complete the change to cylindric form, and remain quiescent during two non-feeding instars, before transforming to pupae. Their spinning powers are employed in the making of cocoons.

In these later instars there is a gradation through the Gracilariidae in the degree of development of legs. In the external feeding stages the Gracilara and its near allies the legs and prolegs have as great a development as in other larvae that are free-feeding from birth. In some members of the Lithocolletis groups they are fairly well developed. In the fourth and fifth and even sixth and seventh stages of the Cameraria group they are very little developed indeed, the thoracic legs often being reduced to mere disc-like

vestiges and the prolegs showing as hardly more than a circlet of crochets on the integument.

The pupae of all the Gracilariidae have considerable power of movement. If touched in their retreats a vigorous reaction may be set up in which they bend the abdomen and roll from side to side. When the adults are ready to emerge they become active within the shells and force an exit aided by the free segments in the abdomen, a cutting crest or plate on the head and backward pointing spines. When the pupal shell is pushed out far enough and comes to rest on the leaf or cocoon surface with only the hinder segments remaining in the emergence hole, then its skin splits and the adult is freed. And often the adult is an exquisite little creature, arrayed in shining scales and plumes, its wings overlaid with glistening silver or burnished gold.

The size of the family and the range of its food plants will be learned by consulting our lists in Chapters XV and XVI. They are so numerous that we can use but a few typical representatives of the principal genera for illustration.

PARORNIX

This is a genus of more than a dozen species of leaf-miners that show a partiality for plants of the rose family. The very young larvae of the genus Parornix mine by shearing through the cell walls of a single layer of parenchymous tissue nearest the cuticle. In this genus the lower side of the leaves is the one attacked. After assuming more nearly normal head capsules and mouth parts at the second moult they usually continue in the leaf for a while, picking out the parenchyma from the exposed tissue. When nearly grown they emerge from the leaves and feed within a shelter made by turning and binding down the border of a leaf. The fold made by members of this genus, unlike that made by species of Gracilaria, is more often flat than cone-shaped. In some such fold the cocoons are later spun though it is

not always in the one made upon emerging from the leaf nor is it always as tightly bound down as in the feeding shelter.

In form the larvae are subcylindrical. They are often marked by four black spots upon the upper surface of the prothorax. The cocoons spun by larvae of this genus are different from those of most related genera in that they are usually reddish or brownish in color and somewhat mottled. In texture they are firm and opaque.

Over-wintering cocoons are spun in the fall and adults usually emerge from these in May, the pupal shells being thrust through the cocoons in their release. There are several broods each season.

The unspotted tentiform leaf-miner of the apple, Parornix prunivorella is a very common miner of apples, cherries and other woody rosaceous plants. It is known from the Atlantic States westward at least as far as Missouri. The adults, small, dark, steelgray moths 7 to 9 mm. in expanse, emerge in early spring from over-wintering cocoons. They soon lay eggs, and from then until late autumn moths or caterpillars may be found. In Missouri, Dr. L. Haseman says that there are five fairly well marked generations during the summer months, each one requiring about four weeks for its development. Farther north the generations are not so many.

The eggs are deposited during the evening or at night. They are to be found singly on the lower surface of the leaves. They are slightly oval in outline, flattened and exceedingly small, being but 0.25 to 0.4 mm. in length. They are finely sculptured over the whole surface but on the side next the leaf the marking is somewhat obscured by its pressure against the leaf and by the cement attaching it to the cuticle, and form a sort of ball which is suspended from the walls with silk.

In the later stages the head capsule is marked with four

black spots above, and on the dorsum of the prothorax are four similar, but slightly larger black spots. The head-capsule is brownish and the body greenish gray with rows of white tubercles bearing prominent hairs.

When the parenchyma of the mine wall is consumed the larvae emerge from the leaves through small holes in the lower side of the mines and crawl about in search of a suitable place to pupate. Sometimes they fold over a portion of the leaf border and feed there to a slight extent but more often they feed no more before spinning the cocoon. Previous to pupation the larvae draw over a portion of the leaf border by spinning silk cords from it to the leaf. They then line this fold with silk and spin a sheet across the gap making a firm, opaque, reddish-brown cocoon. Within the cocoons they change to pupae. A week or ten days later the pupal shells are thrust through the cocoon walls as the adults emerge.

Gracilaria

This is a large genus of very similar and very variable species, that are difficult of determination without knowledge of the food plants on which they have been reared.[2] The young larvae of Gracilaria are all miners but most of them emerge from the mine as normal larvae and feed on the outside of the leaf. They never live as exposed feeders, however, but make shelters for themselves by spinning silk in such a way as to cause the leaf to bend or curl over them. In some species the curling is clumsily done so that the leaf is half crumpled. This is the case with lilac leaves attacked by a common European species, *G. syringella*, now introduced in this country. Other species make very neat cones, strapping the tip of the leaf down to one border and later spinning again to fold this over into a helix. Some-

[2] Forbes (1923, pp. 170–171) gives a synopsis by foods for the species of the northeastern United States.

times the leaf is cut and a cone made from a pointed flap of it. Some larvae feed on the upper surface and bend the tip upward while other species cause it to bend downward. The pupal case is a stout cocoon of silk spun within the shelter of this cone.

The willow-leaf cone-maker, Gracilaria stigmatella. The young larvae of *G. stigmatella* separate the upper cuticle of the leaves of willows or of poplars. They make at first a short linear mine and then a blotch somewhat toward the tip of the leaf. In later life the larvae emerge and by means of silk draw the tip of the leaf upward and over until it lies on one margin and forms a triangular fold or cone. Thus a sort of spiral is begun. Especially in the willows with slenderer leaves a helix of three coils may be formed involving the whole leaf to the base. The larvae live in these shelters and feed on their inner surfaces. These later stage cylindrical larvae are very like other free-feeding larvae in form but perhaps have a somewhat narrower head. They are uniformly greenish-yellow in color even to the segmental appendages and attain a length of 6 to 7 mm.

Often they pupate in the cone but sometimes they go to the ground where they envelop themselves in a dense semi-transparent web.

The box-elder leaf-roller, Gracilaria negundella. This is one of the most common and widely distributed members of its genus. It is known at least from Colorado to New Jersey. Its range has doubtless been extended in the East by the extensive planting of this tree for shade and ornament. Some of the trees observed by one of us (Mrs. Tothill) in Lake County, Illinois, in the summer of 1916 seemed to have one or two mines in every leaf. It has at times been reported as very abundant in Missouri.

When the minute flat-headed, flat-bodied larvae of this moth begin to mine they separate the upper cuticle from the parenchymous tissue in a contorted linear tract hardly

wider than their own small bodies. This part of the mine is notable for its erratic angling and bending. Moreover, here and there are a few narrow branches from this linear tract which end blindly and so narrowly that it seems that no larva could have turned around in their narrow confines, but rather that, arriving at the place where these end so abruptly they had capriciously changed their minds about the way they wished to go and had slipped backward, to start at another point in another direction. This linear portion of the mine is a few centimeters in length. The character of the mine then changes to a blotch but the larvae still feed on sap and shear through only one layer of cells. The blotch is irregular in shape being somewhat influenced by the position of the veins. In area it is somewhat less than half a square centimeter. The frass of all this sap-feeding period of mining is finely divided and adheres in rather smeared particles to the upper cuticle of the mine—for the larva does this part of the mining while lying on its back.

After a second moult the larval form changes to one very much more like that of a normal free-living caterpillar, the head capsule becoming oblique to the plane of the body. The larvae are still very small, being less than 2 mm. in length. They loiter for a while in the confines of the blotch, move around, now with the venter down, and pick out parenchymous tissue from between the tiny veins in the floor of the mine. The excrement of this period is in more definitely rounded and larger particles which seem to be dryer at the time of deposition for they no longer adhere to the wall of the mine. They are more or less collected into one of the places cleared of parenchyma and they are slightly webbed together with silk.

When only a little more than half of the parenchyma has been removed—picked in little patches here and there from the floor of the mine—the larvae moult again. After

this moult they emerge from the mines and going to the tip of one of the lobes turn it back upon the lower surface by attaching it there with silk. They spin a web at the border of this bent-over portion and use it as a shelter within which to feed. They eat away the soft tissue of the

FIG. 39

FIG. 40

FIG. 39. Leaf of box elder with a mine of *Gracilaria negundella* in one leaflet, and a cone (rolled up) in another leaflet.

FIG. 40. Diagram of a chestnut leaf with a normal mine of *Acrocercops strigifinitella*. (In part after Heinrich and De Gryse.) *e*, egg and entrance hole; *1* and *2*, the course of the first two sap-feeding larval instars through the leaf membrane; *3*, the course of the third, transition instar down a lateral vein; *4* and *5*, the course of the later, tissue-feeding instars in the mid rib, *x*, exit hole.

enclosure leaving only a skeleton and the upper cuticle. Before all the tissue is removed from the interior of this shelter—a portion is seemingly retained for protection—the larvae may cause a second bend to occur, turning the end of the lobe about a centimeter farther back. The excre-

ment of this leaf-rolling period continues to be deposited in rather dry rounded globules and is somewhat localized within the shelter. When a large share of the soft tissue has been removed from the inner walls of this larger enclosure with perhaps a little accessory tissue reached from beyond its borders, the larvae prepare for pupation. They spin rather dense and tough elongate, whitish cocoons within the feeding shelter and presently cast their last larval skins revealing a slender motile pupa with backwardly pointing spines and a serrated cutting plate upon the ventral surface of the head. These structures assist later in forcing the pupal shell through the cocoon and encircling leaf tissues to allow the emergence of the adult.

Acrocercops

This is a small group of leaf-miners whose larvae have two, flat, sap-feeding instars, that are followed, so far as known by three that are tissue-feeding. The mines begin variously, at first being irregularly serpentine, but sooner or later they widen into a blotch. The pupa is formed either within or outside the mine.

The *strigifin miner, A. strigifinitella,* is the species whose habits are best known. It is especially interesting, though perhaps a bit aberrant, in its gradual shift from the flat to the cylindric form of larva. We quote as follows from Heinrich and DeGryse's (1915) excellent account of it:

> Chestnut appears to be the favorite food plant and during midsummer the work of the species is very common, few of the young leaves escaping infestation, some bearing as many as four separate mines. When the proper food supply is abundant, however, there is rarely more than one or two to the leaf. There are a number of generations with considerable overlapping so that larvae are to be found any time from May till well on into October. The first larval brood appears in spring as soon as the leaves are formed. During July and August the dominant period in the

seasonal life of the species is reached. Towards fall there is a gradual diminution in numbers, and during October a partial dying out of the species, due in great measure to the scarcity of new leaves which are necessary to the successful maturing of the larvae. In the neighborhood of Washington, D. C., the last larval brood appears early in October.

The eggs are laid singly on the under surface of the leaves, usually near the base and between the branching ribs. They average about 0.1 mm. in length, are elliptic in circumference, flattened below and convex above, shining pearly white, and minutely faceted. The period of incubation for those specimens under observation was from 4 to 6 days.

Upon emergence from the egg the young larva makes a short irregular linear mine just beneath the cuticle of the leaf on the under side. In this mine it passes the first two instars during both of which it is of the flat specialized gracilariid type, whitish, without legs, abdominal feet or discernible body tubercles or setae.

After the larva has moulted for the second time it bores into one of the branching ribs which it mines during the whole or greater part of the third instar. The later instars, two of which we are able to account for, are passed in the mid-rib within which the larva mines up or down, as the case may be, and from which it emerges when ready to spin its cocoon. As a rule the path of the mine is upward, the larva emerging from the upper side of the rib near the tip. In some cases where the leaf is too small for the mid-rib to afford sufficient nourishment, the larva continues to mine from there into the fleshy part of the leaf making a large irregular blotch quite similar to that of *Eriocrania*. This habit, however, is quite abnormal.

The first two instars are the only ones in which the larvea are of the flat gracilariid type. The third instar larva is transitional between these and the typical cylindrical gracilariid form of the following instars, but with pronounced affinities to the latter. It is cylindrical, has well developed spinneret, labial and maxillary palpi and appreciable body setae. There are, however, no noticeable legs or abdominal feet and the head-capsule while rounded inclines somewhat to the flattened wedge shape.

The mature larva is in general body characters typical of the family. It is whitish, or, when it has fed up in the blotch mine, greenish, without color markings. The abdominal feet bear seven crochets in two curved rows all pointing backward. Length of full grown larva, 6 to 7 mm. The entire larval period is about twenty days.

After it leaves its mine the larva lets itself down by a strand of silk to a more secluded place where it spins a cocoon, nearly always on the under side of a leaf near the edge or against one of the ribs. The cocoon is a double affair consisting of a thin outer layer built up from the leaf, and a second, similar, inner layer, everywhere separated from the first by from 1 to 1.5 mm. The cocoon is 14 mm. long, white, rather flattened, oval and transparent. The outer covering is decorated along the middle with from four to ten small, pearl-like globules similar to those on the Marmara cocoons, but fewer in number and less brilliant.

Within its silken enclosure the pupa is plainly visible. Throughout the pupal period it is noticeably active, revolving rapidly on the axis of the body when disturbed; greenish brown and structurally normal. The pupal period is six to ten days in summer.

The adult is a grayish-brown moth with a wing expanse of a third of an inch (8 mm.) Its yellowish white palpi are ringed with brown, and its grayish-brown fore wings are obliquely streaked inward from both margins with white.

In summer the entire life cycle of the insect from egg to imago, is completed in a trifle over a month.

Apophthisis

A single species of this genus *A. pullata*, reared by Miss Braun near Cincinnati, Ohio, and first described by her, differs in having the mine at first deep in the tissue. The mine, she says, lies deep in the leaf substance of buckthorn, *Rhamnus lanceolata* Pursh. It is linear at first, gradually broadening into an irregular blotch 5 or 6 mm. wide, occupying about one-fourth the area of the leaf. The leaf retains its green color so that the mine is not clearly visible during

the early stages. In the later portions of the blotch the substance of the leaf is consumed, rendering the mine distinct.

The pupa is in a broadly oval, flat, yellow cocoon spun in a fold of the leaf or in a crevice. There are two generations a year. The larvae that mine in early July emerge as

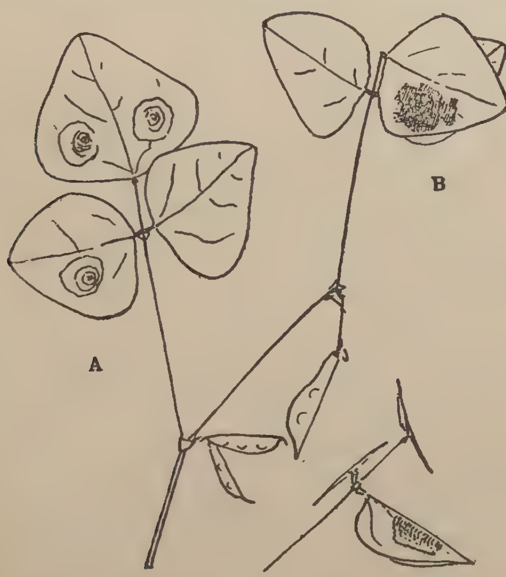


FIG. 41. A spray of hog-peanut with three types of leaf injuries. *A*, flat blotch mines of *Leucanthiza amphicarpeaefoliella; B*, a shelter between two leaflets made by the leaf-sewer, *Stilbosis tesquella,* within which mainly the tissues of the uppermost leaflet are excavated; *C*, a tentiform blotch mine of *Lithocolletis morrisella.*

adults in late summer, hibernate as pupae and emerge in early spring.

Leucanthiza

This is a small genus in which the larvae do all their feeding in the mine and emerge just before spinning their cocoons. The mines are irregular blotches on the upper surface of the leaves.

The leatherwood leaf-miner, L. dircella, mines the leaves of *Dirca palustris.* It makes large, white blotches on the upper surface and from one to eight larvae may be found in a single mine. When the larvae are gregarious in a mine most of the leaf is involved and the several individuals occupy finger-like projections at the borders of the mine. Larvae may be found in the leaves in June and in September in the latitude of southern Ohio. The cocoons are spun outside of the mine.

The hog-peanut leaf-miner, L. amphicarpeaefoliella, mines the leaves of *Falcata monoica* and *F. pitcheri* from August to October. The larvae make creamy white blotches covering most of the upper surfaces of the leaves. When full-fed they cast their last moult skins and emerge to spin cocoons in withered leaves or on the ground.

Marmara

This is a genus of about a dozen North American species, whose flat, sap-feeding larvae are miners for the most part, not in leaves but under the cuticle of young twigs or of semi-herbaceous stems. Two species are leaf-miners, and a third mines under the cuticle of the joints of prickly pear (Opuntia): these joints are functionally comparable with leaves. One species, *M. pomonella,* has been recorded by Knight (1922) as damaging the appearance of apples by mining their surface when green (see pl. 2, fig. 4).

A possible explanation of their departure from family habit is that, in the course of evolution, the seasonal development became so changed that the maturation of eggs was no longer synchronous with the leafy season of the host plants, and that the adults met the emergency by ovipositing on the next most succulent part. Certain it is that *M. salictella* now mines willow shoots and *M. fulgidella* the branches of oak in the early spring before the leaf buds have opened. Also, the species, that are leaf-miners have, as

hosts, plants with evergreen leaves. Opuntia joints also are evergreen.

Whether found in shoots, prickly pear joints or leaves, the mines of species of this genus are very long, very narrow, more or less winding and, at least for most of their length, involve but a single layer of parenchyma cells. The larvae leave the mines to pupate. The cocoons of the leaf-mining species are characteristic, of white or yellowish silk, and unusual in that they are decorated with a good many iridescent or pearly white globules.

The smilax miner, Marmara smilacisella, works in the leaves of several species of the genus Smilax, some of which are commonly known as cat briers. Miss Braun found it on *Smilax hispida* about Cincinnati, Ohio. She says that it mines the upper side of the leaves, making a silvery white narrow mine which even in its latter stages is no more than 2.5 mm. wide. There is a narrow central line of frass. The mines wind about over the leaf, crossing and recrossing and in smaller leaves involving almost the whole upper surface.

At maturity the larvae turn bright red, emerge from the mine, and, in a fold under the edge of the leaf, spin yellowish white cocoons with groups of the iridescent globules at the ends.

The arbutus miner, Marmara arbutiella, one of us (Mrs. Tothill) has observed working on the Madrona tree, *Arbutus menziesii,* in British Columbia, and extracts from her notes have already been given in the introduction to this book (p. 26). She noted further that mines made by these larvae are very characteristic in appearance, for with their cell-shearing mandibles they sever the cuticle of the leaf from its parenchyma so adroitly that the colorless epidermis is left almost "chemically clean." The mine, therefore, appears by reflected light to be a solid white line.

In the first collection of mines of this species, made about

mid-April from succulent saplings in a semi-open field, the mines were already some ten to fifteen or twenty centimeters in length and were about evenly distributed over stems and leaves, and were developed on both the upper and the under surfaces of the leaves. Later they were found on mature trees, in which the nodes and leaves were crowded on the very much shortened shoots of the year, the mines were to be found only in the leaves; and they then conformed very closely to the hitherto published descriptions.

The larvae of the first brood remain in the mines until late June or early July. The galleries increase in width very very slowly but in length they increase rapidly, and wind about crossing and recrossing until they involve much of the upper surface. The later portion of the mines is yellowish in color and from 2 to 5 mm. wide.

The cocoon is spun in a curled leaf, or in a crevice of curls, and is characteristic of the genus. There is a sheet of white silk spun over the larval retreat. This is slightly irregular in outline and about one-fourth inch in diameter and partially transparent. When the sheet is complete holes are made in it by the larva which then decorates the exterior with tiny bunches of iridescent white globules that are like toy balloons for fairies. The holes are probably made by the mouthparts, and the material which forms the globules is probably secreted by the Malpighian tubules and extruded through the anal opening.

The pupae are yellow in appearance and are found soon after the cocoons are complete.

The adults emerge after the middle of July when the new shoots and leaves of the Madrona are well developed.

Parecopta

The members of this small genus remain as larvae within their mines until full-fed and then emerge to spin dense, semi-transparent, somewhat flattened, white cocoons in a

fold of the leaf, or in some crevice, or on the ground. There are two types of mines. The miners that work on legumes and on willows make digitate, flat, pale yellow mines. Those

FIG. 42. The work of the digitate leaf-miner of the locust, *Parectopa robiniella*. *A*, upper side of locust leaf with a number of mines; *B*, under side view of a single leaflet, torn open to show the frass neatly packed away in a vault, so to speak, and the passage-way to the upper-side mine, which is clean.

that work on plants of the Compositae make at first narrow winding frass-filled mines, which later become blotched and expanded bladderlike, with both layers of epidermis puffed out.

The digitate-mine-maker of the locust, P. robiniella, is a common and widely distributed species. It attacks the leaves of locusts and of other legumes. The mines may be found from early summer until late fall. They are first extended along the midribs of the leaves as narrow tracts and then into the area on either side by a series of finger-like excavations. Previous to mining the upper side, however, a very small subcuticular mine is made next the midrib on the lower side. From this a passage is made to the opening under the upper cuticle where the upper side mine begins. During their whole period of mining the larvae return to these slits and through them extrude their excrement. Even moulted skins may be found packed in with the frass in the little lowerside mines. This combination of a large, clean-swept upper side mine with a small lower side storage vault is distinctive, but the peculiar shape of the upper side mine will alone identify these miners.

In the later larval stages a considerable portion of the parenchyma of the leaf is removed. Indeed, we have seen leaves in which these mines overlapped those of *Lithocolletis robiniella* on the lower surface of the leaf, and yet between the two mines there was an unperforated sheet of fibrovascular tissue and parenchyma. The mines are of a yellow color; the mine of *Lithocolletis robiniella* is pearly white.

The larvae leave the mines when full-fed; at that time they are cylindrical and pale green, with legs and prolegs well developed. In a fold of a leaf or in some crevice (or even, spread out upon the glass when captured in a bottle), the larvae spin a transparent somewhat flattened oval cocoon.

Cremastobombycia

This is a small group of species whose larvae are sap-feeders during the first three instars, and tissue-feeders within the mine thereafter. While their mandibles are of

Lepidopterous Leaf-Miners

Fig. 1. Maple leaf, bearing mines of *Lithocolletis aceriella.* (From Slingerland Collection.)

Fig. 2. Apple leaf, bearing mines of *Bucculatrix pomifoliella;* also several molting cocoons. (After Slingerland and Crosby.)

Fig. 3. Plum leaf, bearing a number of mines of *Nepticula slingerlandella.* (After Crosby.)

the cell-shearing type they separate the epidermis of the lower side of the leaves. Then they spin silk to cause the epidermis to become wrinkled, and feed afterward upon the parenchyma of the arched side of the mine. They all live in the leaves of herbaceous composites.

In preparing for pupation the larvae of this division spin elongate white cocoons smooth or ridged from end to end. These are suspended in the mine in a very characteristic hammock-like way by two slightly diverging silken threads at the posterior end and one or two threads at the anterior end. The pupae penetrate through these cocoons and through the leaf tissues just before the adults are freed.

The goldenrod leaf-miner, C. solidaginis, is one of the commoner species in the United States. It mines the underside of the leaves of species of goldenrod, making elongate much wrinkled mines. The cocoons spun by this species are dense and white marked with longitudinal ridges. They are suspended in the mine by a single silken thread at the anterior end and by two diverging threads at the posterior end.

Lithocolletis[3]

This is the greatest genus of leaf-miners in the world. Some 200 species have been described from North America alone, and, doubtless, there are others still unknown. They probably outnumber all remaining leaf-mining Lepidoptera together. The world is full of them. If any one would find them for himself he has only to search for a few moments the green leaves of such trees as oaks, witch hazel, lindens and birches. Our lists will show (p. 317) that they have a marked predilation for oaks, hornbeam and nut-bearing trees, and that few of them infest herbaceous plants. Both larval and pupal stages are passed within the mine. During the first three instars the larvae are of the flat, sap-feed-

[3] Called also *Phyllonorycter*.

ing type, being equipped with cell-shearing mandibles. In subsequent instars they feed more or less extensively upon the tissues, and spin silken threads across the loosened cuticle, causing the surface to become more or less ridged or tentiform.

There are two rather well marked groups of species within the genus:

1. The Lithocolletis group proper.
2. The Cameraria group.

The adults of these two groups differ but slightly, and only in color, so far as noted. The white streakings of the wings in the former group are dark-margined internally while in the latter they are dark-margined externally. The pupae differ in that a cremaster is always developed at the caudal extremity of the body in the former, while in the pupae of the latter there is none.

The larvae of the two groups differ rather remarkably. They differ both in form and habit. In the group of Lithocolletis proper, after the change from the flat, sap-feeding beginning, they are cylindrical in the fourth and later instars, with the head of the form of ordinary free-living caterpillars. In the Cameraria group the larvae after the third and last sap-feeding instar, continue to be depressed and distinctly flattened in form, though less flat than before, and the long axis of the head capsule continues in the same plane with that of the body, and has the mouthparts protruding in front. They further differ from first group larvae in having dark bars or maculae laid across most of the body segments both above and below. On account of this difference of form, in the larval stages that are most commonly seen, they often become designated as "cylindric group" and "flat group" larvae.

Larvae of the first or cylindric group during their fourth and fifth instars pick out the parenchyma from the network of veins on the arched side of the mine, removing all the

soft leaf tissue, one face of which was sheared free from the epidermis in the earlier sap-feeding instars. They thus complete the removal of this tissue, without much altering the outer borders of the mine; and often during three later instars they feed from the periphery toward the center, and bestow their granular frass at the outer edges.

The larva of the second or flat (Cameraria) group, in the fourth and fifth instars, instead of picking out parenchyma from already exposed tissue, continue to extend their mines, now by cutting out thin sheets of tissue beyond the former periphery. They are peculiar in having seven instars, of which the last two are non-feeding stages in which the larvae merely prepare for pupation.

The mines made by the larvae of the first group may be oval, or circular, or nearly rectangular, bounded by veins. In removing the parenchyma most of the larvae feed from the circumference inwards. Some begin at one end and work toward the other, and some, as *L. crataegella* on apples, pick it out irregularly in spots. The frass of the tissue-feeding instars may be collected into a ball, or scattered about tidily around the periphery of the mine.

All the larvae in this first group pupate in the mines[4] and may or may not first enclose themselves in cocoons. In the species in which no definite cocoon is made, the pupae may be suspended by a thin meshwork of silken threads as in *L. fitchella, L. argentifimbriella, L. clemensella* and *L. lucidocostella,* or the part of the mine containing the pupa may be sparingly lined with silk, as is the mine of *L. martiella.* The naked pupae of *L. populiella* are said to be attached by their anal ends to a button of silk on the roof of their mines. When a more definite cocoon is made it may be large and loosely woven, taking up nearly half of the mine in the case of *L. albanotella* and *L. robiniella,*

[4] Excepting only (so far as now known) *L. ostensackenella.*

or small and ovoid formed of frass and silk as are those of *L. caryaealbella* and *L. aeriferella*, or merely an oval ring with an outline of frass like that of *L. basistrigella*, or an oval, flattened transparent cell like that of *L. lucetiella*.

In species of the group of Lithocolletis proper the mine is often narrow and somewhat winding at first but it soon

FIG. 43. *Lithocolletis hamadryadella*. (From Comstock.) *a*, mine; *b*, young larva; *c*, full grown flat form larva; *d*, head of same, enlarged; *e*, antenna of same; *f*, round form larva from above; *g*, same from below; *h*, head of same enlarged; *i*, antenna of same; *k*, maxilla and palpus of same; *l*, labum, labial palpi and spinnerets of same; *m*, pupa; *p*, cocoon; *q*, moth.

spreads into a blotch which often involves the part of the leaf which contained the earlier winding portion.

When the larvae assume the cylindrical form in the fourth instar they cease to separate the cuticle and from that time on the outline of the mine does not change. The newly-developed spinneret is usually employed almost at once in spinning silk in sheets or bands under the separated epidermis, and it is the shrinking of this silk in drying which

causes the mines to become tentiform. During the fourth and fifth instars the larvae pick out the parenchyma from the fibrovascular network on the arched side of the mine.

The typical Lithocolletiform mine, with the separated lower epidermis drawn into folds and the parenchymous tissue removed from the arched side, is not always adhered to in this first group. Some species first separate the lower epidermis of leaves, gather it into folds and feed on the arched lower side, and some do not cause the surface of the mine to be arched or tentiform.

The mines of all species of the Cameraria group are on the upper side of the leaves of their host plants. They usually continue to be flat until just before pupation when one or a few slight folds may be made in the upper cuticle. On holding a completed mine to the light its parts will be seen to differ in transparency, the denser portion being that from which the cuticle was removed in the early sap-feeding instars, and the more transparent portion, that part of the mine excavated by the larvae in their fourth and fifth instars.

Very many of the species are gregarious in larval habit, the mines being occupied by several larvae extending the mine at different points on its borders.

The excrement of these larvae is not granular after the third moult but seems usually to be somewhat viscous at the time of deposition and is smeared upon the floor of the mine. It is usually not very localized though in the community mines where the several larvae feed outwardly from the centre, the borders are fairly clean. When solitary larvae make elongate mines the excrement is usually scattered along the middle of the mines. Probably the most peculiar arrangement of excrement in this group is in the mines of *L. tubiferella* on oak. The mines are elongate, and, gradually widening, continue to be about as wide as the larvae are long. The larvae feed first on one side and

then on the other, and their position at the time of feeding being transverse to the course of the mine. The excrement on this account comes to be arranged in two black lines one at either border of the mine its whole length.

There are usually two generations annually of species of the Cameraria group, though there may sometimes be but one. The summer brood pupates as follows: its mine remains flat until the seventh instar. Then as the larvae approach pupation they spin a small amount of silk upon the loosened epidermis, which by contraction causes one to three narrow folds or ridges. Beneath these folds the larva spins a thin sheet of silk over a part of the floor and then lying on its back spins over itself a flat semi-transparent sheet of silk, oval or nearly circular in shape and attached around its edges to the silk-strewn patch below. The larva then comes to rest under the long axis of the cocoon and presently transforms to a pupa. Before the adult escapes the pupal shell is thrust through a transverse slit at one end of the flat cocoon and through the upper cuticle of the leaf. The generation emerging in early summer has overwintered as larvae. In some species, hibernation takes place under the folded epidermis but in most species an especially prepared silk-lined chamber is formed. Oval or rounded silken patches are spun upon corresponding areas to form a unique chamber of silk and cuticle. On the upper side of the leaf it appears as a flat, smooth circle, on the lower as an oval or hemispherical projection. The change to a pupa occurs in the spring.

In choice of host plants in this group resembles that in the group of Lithocolletis proper very strongly. All the recorded host plants of North American species are broad-leaved woody plants. Thirteen species are attached to the oak group, four to the birch family, and the eleven other species whose hosts are recorded are distributed to eight other families containing woody plants.

Out of the vast array of forms with which we might illustrate this great genus, we will select three only, two having cylindric (first group) and one having flat (second group) larvae.

The maple leaf-miner, Lithocolletis lucidicostella, makes mines that are typical of the first group. In the three sap-feeding instars the larvae separate the cuticle of the under side of the leaves unless delimited by large veins are rounded or oval. The rounded mines are but a centimeter and a

FIG. 44. Mines of the maple leaf-miner *Lithocolletes lucidicostella,* with central blackish frass pile. Earlier flat mines shown at *A*; later tentiform mine shown at *B*.

half in area. In the fourth and fifth instars the larvae spin silk upon the separated cuticle making the mine somewhat tentiform and pick out the parenchyma from the exposed tissue of its arched side. Beginning at the extreme periphery of the mine the larvae clean the green tissue from each interstice between the small veins separately and completely as they go and the cleared area is a succession of tiny lattice-like squares. The frass of this period of feeding is collected into a rather firm ball toward one side of the mine. Its mass

varies inversely with the amount of green tissue remaining, until, when the whole mine is cleared, it has a diameter of some 2 to 3 mm. No definite cocoon is made by this species but a web of silk spun across the part of the arch away from the frass-ball supports the pupae.

The polygon miner of the linden, L. lucetiella, is rather common in the Atlantic States. The mines are usually bounded by two main lateral veins and by two of the veins running from one to the other of these. These boundaries give the mine a rectangular, often nearly square outline. The larvae separate the cuticle in their first three instars and in the fourth and fifth, pick out the parenchyma of the area but they do not spin silk upon the separated cuticle and the mine is unusual in being entirely flat. The green tissue is eaten away first at the edges and then more and more towards the center until when the larvae stop feeding the mine is either entirely clear or has but a few flecks of green in the middle. All the excrement of this period is pushed to the extreme borders of the mines, which when complete are shining white and so transparent that the pale greenish larvae can be seen very plainly. In the center of the mines the larvae spin flattened oval cocoons. The ring-like wall between the floor and the roof of the mine is somewhat firm but the sheets of silk spun upon the cuticles are very thin and transparent and the slender motile pupae are plainly visible within.

The brown-blotch leaf-mine of the witch hazel, L. hamameliella, is one of the common miners in regions where its host plant occurs. The larvae make circular or somewhat irregular mines on the upper side of the leaves, two to several larvae inhabiting a single mine. They shear through the upper cells of the leaf in their early stages and in their fourth and fifth stages further extend the mine by the removal of thin slices of tissue. At first the mines are whitish, later somewhat brownish and discolored. The excrementi-

tious matter is smeared in a waxy layer irregularly over the floor of the mine, making it brown and dirty except at the borders where it is fairly clean.

The pupa of the summer brood is formed beneath a flat circular sheet of silk attached at its edges to the lower side of the leaf. The over-wintering larvae prepare the typical hemispherical hibernating chambers described above.

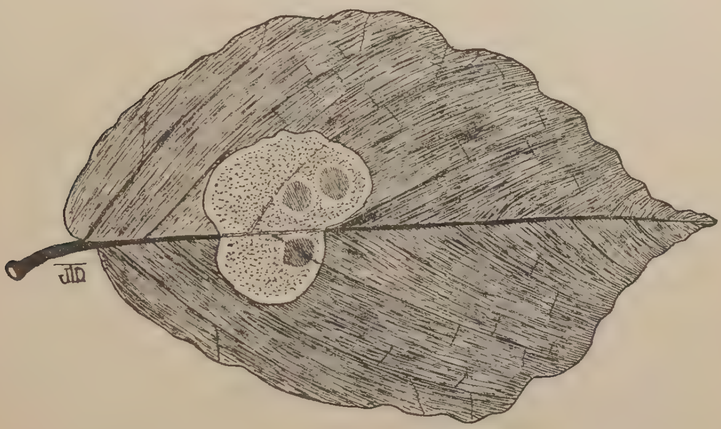


FIG. 45. A brown blotch mine of the witch hazel as seen in autumn, containing three hibernating cocoons.

COLEOPHORIDAE

The case-bearers

This family is represented in North America by a single large genus, Coleophora, containing a hundred or more species, many of which begin life as leaf-miners. Many of them are external feeders, and of these that mine, none dwell within their mines longer than the first instar. All construct portable cases, which they carry on their backs. If they do any mining after constructing cases, they do it as

a rule without leaving their cases, by reaching through a hole in the epidermis, and feeding in a circle as far as they can reach while holding on to their cases in the rear.

Hence, they are ordinary little caterpillars in form, all tissue-feeders, not flattened, nor otherwise specially adapted to leaf-mining.

In development the many species are similar. Of those having a single generation a year, the eggs are laid in summer; the larvae feed and make small cases in which they hibernate; in early spring they feed again for a few weeks; sealing down their cases, they transform to pupae; and the adult insects issue in late spring or early summer. In those that have two generations a year one set of larvae hibernates in a similar way.

The egg. The eggs are never inserted within the plant tissue, though in some seed-and-flower-feeders they are slipped inside unopened florets. They are deposited on the leaf surface. Among the leaf miners of the group there are at least two types of eggs and two modes of entering the leaf, as described under the two illustrative species cited in the following pages.

The larva. The larva (see pl. 2, figs. 7 and 8) are little if at all depressed. The head capsule differs from that of most miners in that the front is not open, the arms of the epicranial suture meeting the stem about a third of the way from the vertex. The adfrontal plates extend to the vertex. The ocelli are all close together. The body is nearly cylindrical. The thoracic legs are well developed and strongly chitinized. Prolegs occur on segments 3, 4, 5, 6 and 10 of the abdomen. These protrude but slightly, and are to be found close to the middle line of the ventral surface so that the hooks, which are in two transverse rows on each proleg, form nearly continuous bands across the central part of the venter. The anal prolegs are better developed than the

others but have only one transverse row of crochets. From observing the larva in action it seems that these bands of hooks act in protruding the larvae and in withdrawing them into their cases. In a few species the number of crochets is much reduced. In *C. fletcherella* they are vestigial, only 2 to 6 being represented on the prolegs other than the anal ones. In *C. limosipennella* they are lacking entirely.

The markings and strong chitinization of the larvae are confined to the parts which are particularly exposed. In walking about the caterpillars protrude the head, and most of the thorax. They have accordingly black, strongly chitinized head capsules, a black bisected prothoracic shield and a pair of black chitinous plates on the following one or two segments. The legs are also well chitinized. As the larvae feed from their cases they move backward from time to time and, thrusting the anal segment through the posterior valves of the cases they extrude excrement. This anal segment is also protected by a large black plate. The spiracles along the sides of the body are small, circular and faintly indicated, those on the eighth segment, according to Fracker, being twice as large as the others and placed somewhat higher on the segment.

The pupa. The pupae are formed within the larval cases. They are dark colored and about four times as long as they are thick. The appendages are soldered one to the other but are free from the body wall. Though abdominal fusion is not entirely complete the seventh segment is fixed in both sexes and the pupal shells are not extruded from the cases at the time of emergence. Though there is no true cremaster, the last abdominal segment bulges out very much at either side and the lateral prolongations are tipped with stout spines. These are caught into the button of silk which seals the case to its support and serves to attach the pupa.

The adult. They are plain little moths, whose wing markings are limited to dustings of lighter and darker scales. In expanse of wings they measure usually less than half an inch.

This genus has considerable economic importance. The destructiveness of the group would be much less were it not that all the larvae hibernate in a late stage of development and in very early spring are ready to do their most destructive feeding just as the host plants are beginning to put forth leaves. At this season those attached to fruit trees, for instance, burrow into leaf and fruit buds or into succulent young growing twigs and in this way cause considerable injury. Fortunately, they are of very small size,

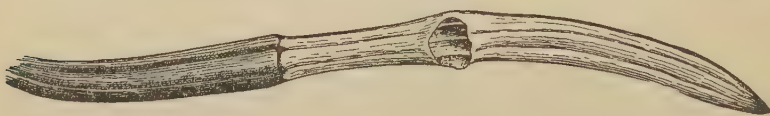


FIG. 46. The work of the larch base-bearer, *Coleophora laricella.* (After Herrick.)

have but one generation a year in most cases, and, despite their protective coverings, are attacked by various hymenopterous parasites, by predacious insects and by birds. In orchards, where artificial measures are practicable, arsenical sprays applied to the foliage or lime-sulphur wash applied before the buds expand diminish their numbers very greatly.

The larch case-bearer, coleophora laricella, now very common in the eastern parts of the United States and Canada, has been imported from Europe where it is apparently native. It was doubtless introduced here with the Eurpean larch. *Larix europea,* but it has spread to our common native, *Larix americana.* On this continent it was first reported in 1886 from Massachusetts by Dr. Hagen. Now it is found from the Atlantic seaboard inland at least

as far as central New York and eastern Ontario. When abundant the tips of the mined leaves shrivel away and the trees assume the aspect of being severely frosted. From some observations at Ithaca in 1912, Professor Herrick estimated that a single larva may eat or injure as many as a hundred different leaves after becoming active in the spring. What then must have been the severity of the attack on larches in Sweden in which Ivar Traegardh counted as many as twenty-seven, forty-one, and even seventy-four cases hibernating beside single buds!

The moths are small and silvery grayish brown without conspicuous markings. In the northeastern United States they issue during late May or early June. Mating soon takes place and the eggs are deposited on the leaves within a week or ten days after emergence.

The eggs are small, having about a third the diameter of the leaves, but are plainly visible to the naked eye. In color they are reddish brown. Their shape is that of shallow inverted bowls, with a depression at the apex and twelve to fourteen rather bold ridges radiating down the sides. In hatching the larvae bore through the base of the egg directly through the leaf cuticle into the interior, thus avoiding exposure on the surface of the leaf. They begin to mine, at first very slowly, and remain in this single leaf from late June until September. The needles containing the larvae become somewhat transparent and russetted during late summer. The excrement of this period is packed into one end of the mine.

In September the larvae prepare their first cases which they later use as hibernating chambers. For these they either use the leaves in which they have been living during the summer, cutting off the distal end and clearing out the excrement, or they leave these mines and burrow into fresh needles before making a case. Having cleaned the burrow

and lined it with a thin sheet of silk, the larva go to the end of the mine towards the base of the leaf and sever the mined from the unmined portion. They then thrust forth head and legs and travel about wearing the modified burrow as a protecting case. For three or four weeks in the fall they continue to feed. They now attach the rounded mouth of the case to the needles with silk, pierce the cuticle and devour the leaf substance as far as they can reach in either direction. While working from the cases the larvae back up from time to time, and, thrusting the anal segment through the posterior opening of the case, void their excrement. When the larvae can obtain no more food without leaving the case entirely they sever their moorings, move to another leaf and proceed as before. Each larva may mine thoroughly more than one leaf after forming its case and before going into hibernation but unless the insects are exceedingly numerous, their work is inconspicuous at this season.

In October they cease to feed and, shortly before the needles drop, move to the branches. There, often in the axil of a bud, they fasten their cases with a copious supply of silk, close the anal opening with a sheet of silk and become inactive. Though the larch needles are flat the clustered or separated cases are cylindrical, the lining of silk and the shape and activity of the larvae having caused the bulging of the flat surfaces. The larvae at this time have reached a fourth to a third of their ultimate size and are much smaller than their cases in which they can turn and twist about with ease. The cases are an eighth to a sixth of an inch in length.

In the spring when the larch buds begin to swell the larvae awake from their long sleep enhungered; so, loosening themselves from the branches, they at once burrow into the young leaves. Back on the twigs, where the cases are

attached, may be found the black head capsules and perhaps also the body casts of their last moults still adhering to the buttons of silk.

Feeding, they now grow rapidly and soon set about enlarging their cases. To do this they make a slit along the under side and there spin a gusset or a gore of silk. They increase the length by spinning on silk at the anterior end. Later when the leaves have attained considerable length they mine out the interior of one which they cut off and attach over the gore of silk. With such additions and modifications these same cases accommodate them during the remainder of their immature stages. The spring feeding period in the northeastern United States extends for some time in the latter half of April through the first week in May.

When the larvae are full-fed they are from 4.5 to 5 mm. long, brownish in color and marked with black plates on the pro- and mesothoracic and anal segments. They move to the bases of the short side branches or to the centers of the leaf whorls and fastening the cases securely and turning around with the head toward the anal opening of the sheath, transform to small, black pupae. The moths emerge in 14 to 20 days and the life cycle begins again.

The cigar case-bearer of apple, Coleophora fletcherella, is perhaps the best known and most widely distributed of our native species of leaf-mining Coleophoras.

The native hosts of this species are the crab and the hawthorn. With the introduction of European fruit trees and the extensive cultivation of orchards it has found in the pear and apple favorite food plants, though it is sometimes found on quince, plum, and perhaps other species.

The eggs are almost round and minute—measuring about 0.31 by 0.25 mm. They are pale yellow and closely marked with ridges. They are deposited on the leaves in early

July and are most often to be found among the hairs on the under side, particularly along the midrib.

After two weeks (i.e., towards the end of July) the eggs hatch. The larvae do not enter the leaves directly through the egg shells but come out on the side of the eggs and move about on the surface of the leaves for several hours before obtaining an entrance. They live as miners within the leaves for about fourteen days making elliptical brown mines and ejecting from them black powdery excrement. About the first week of August in the northeastern United States they form their first cases, cutting elliptical pieces from the upper and lower walls of the mine and sewing them together. Moving off the leaves in mid September they seal the mouths of these sheaths firmly to the branches and remain until spring as minute half-grown caterpillars.

As soon as the buds begin to swell in the spring the larvae move out upon them and bore into the succulent expanding tissues. Later when these are partially unfolded they attack the young leaves, the stems of flower or fruit, or the downy growing twigs. They feed and grow rapidly, and they prolong one side of the elliptical case into a tube of fragments of tissue and silk. By the time this tube equals or exceeds the original length of the elliptical case the leaves are fully expanded and their cuticles fairly resistant. The larvae then begin to mine from the cases and from one of the earliest mines make a new case.

They attach the cases to the leaf and begin to mine in the usual way but instead of making a small rounded or polygonal mine with the feeding puncture near the center, they make a larger one and get away from the case entirely. The new cases which they cut from the upper and lower cuticles of these mines are in shape very unlike their first ones. At first they are elongate and flattened but as the larvae move about in them and line them with silk they become more

cylindrical or cigar-shaped. The anterior end is round, slightly funnel-form and bent downward so that the plane of the opening forms an acute angle with the long axis of the case. The posterior end has such a shape as might be given the end of a plastic cylinder by pinching it between two fingers and the thumb, the three lobes neatly closing the opening (see pl. 2, fig. 8).

After making these cases the larvae mine from their shelters for about a month. Though they consume even a larger quantity of food their work is probably less injurious at this time than when they are mutilating the buds.

About the middle of June when the larvae become full-fed they are from 5 to 5.3 mm. in length and 1.16 mm. in greatest width. The ground color of the body is reddish-orange. The usual sort of plates occur on the three thoracic and on the anal segments. There are also small lateral plates on the thoracic segments.

Before pupation the cases are firmly sealed to the branches and stand out from them almost at right angles. The larvae then turn around with their heads towards the anal valve and in a day or two transform to typical Coleophora pupae. These are attached by the lateral spine projections of the last segment to the button of silk on the twigs. The pupal stage lasts from ten to twelve days.

The yellowish steel-gray adults make their escape by pushing between the three lobes which close the posterior opening of the case. According to Mr. A. G. Hammer they emerge most often in early afternoon and then for several hours sit on the cases in a characteristic pose, facing away from the branch with their wings folded over their bodies and down over the sides of the case, their long slender antennae pointing directly forward. Though they become restless towards evening and fly about they return to perch upon the cases.

A native species having a similar life history that has come to have some economic importance through the cultivation of pecans is the Pecan or Hickory case-bearer, *Coleophora caryaefoliella.* Its hosts are nut-bearing trees—namely, walnut, pecan, hickory and possibly other related species. Its habits, development, and injuries parallel those of the species just discussed.

CHAPTER VIII

Superfamily Cynodioidea

FAMILY CYCNODIIDAE

The grass miners

This is a small family whose larva mine in the leaves of the coarser grasses and grass-like plants (sedges and bulrushes). Most species appear to be single-brooded and to reach maturity in spring or early summer. From March to May is the best season for finding them. They overwinter as young larvae or as eggs. The mines of those that begin activity in autumn are formed in leaves that later are winter killed; so, in the spring they enter other leaves and make new, and generally larger mines. The mines usually extend from the leaf tip downwards, and naturally they are linear, conforming to the shape of the leaves; but they widen into more or less of a blotch, with the detached epidermis either smooth or wrinkled in the later stages. The pupa is found outside the mine, attached to the leaf, either naked or suspended in a few tangled threads of silk.

The *white hystrix miner, Aphelosetia orestella,* is a common representative of the group. According to Miss Braun (20 and 21) it mines the basal overwintering leaves of the grass *Hystrix patula,* and when these leaves are frozen it transfers to mine new leaves in the spring. The mine extends from the tip of the leaf blade downward, broadening somewhat below. At about the middle of the grayish mine the epidermis is wrinkled, drawing the leaf into a fold. In color it is grayish, as is also the grown larva found within it in the spring. The pupa is not inclosed in a cocoon, but attached flat to the leaf, with head upward.

Concerning the bulrush leaf-miner, *A. robusta,* Miss Braun (21) writes:

> The larvae begin to mine early in April. The mine extends toward the tip of the leaf, beginning as a small transparent blotch, with an opening on the under side of the leaf; following this is a linear green portion with sides nearly parallel, in which the leaf substance is not eaten; beyond this the mine expands and becomes larger and semi-transparent. When ready to pupate, the larva leaves the mine through a circular hole in the upper side of the linear green portion. Larva whitish with head black, thoracic plate dark brown, a brown spot on posterior half of 9 and anterior half of 10. The imagoes emerge in early June.

DOUGLASIIDAE

The little that is known concerning the few leaf miners of this small family is contained in brief and scattered notes on Europaean species; and these notes indicate merely that the larvae are miners during their earliest instars in the leaves of Rosaceous plants, such as strawberry and raspberry.

HELIOZELIDAE

The larvae of this small family are tissue-feeders that eat out the mesophyll rather completely from their small blotch mines, and fill a considerable part of them with their rather voluminous frass. When fully grown they construct lenticular cases from the epidermis of the newer clean portion of the mines, and pupate within these cases. They leave the mine only when they are full-fed. None are known to be case-bearing from the beginning.

The larvae are strongly flattened. They have neither segmented thoracic legs nor prolegs with crochets, but Coptodisca has pairs of little sucker-like discs on thoracic segments two and three, and is able to carry its case some distance before pupating. The pupa has segments 2 to 7 free.

LEPIDOPTEROUS LEAF-MINERS

(All photographs except Fig. 4 from Slingerland Collection, Cornell University)

FIG. 1. Dogwood leaves bearing mines and leaf rolls of *Gracilaria* sp.? The empty pupal skin protudes from the one on the right. FIG. 2. Plum leaf heavily infested by the Trumpet leaf-miner *Tischeria malifoliella*. Note the concentric lines of frass. FIG. 3. One of these same mines more enlarged. FIG. 4. A mine of *Marmara pomonella* in the skin of an apple. (After Knight.) Fig. 5. A spray of arbor-vitae mined by the larva of *Argyresthia thuiella*. FIG. 6. Apple twigs bearing hibernating cases of *Coptodisca splendoriferella*. These cases are cut from the mines. FIG. 7. Larvae of *Coleophora fletcherella*. The largest one bears a Hymenopterous parasite on its back. Fig. 8. A spray of apple bearing these same larvae in their cases. One of the mines shows in the lowest leaf.

Heliozela

In the introductory chapter (p. 24) we have spoken of the habits of *Heliozela aesella,* interesting because they involve both gall-making and gall-consuming, along with case bearing. Of the larvae of the genus Heliozela known in Europe, *H. stanella* first mines in the thickened petioles of oak leaves and afterwards passes up into the leaf blade where it makes a mine and cuts out a case. *H. hammoniella* mines in the twigs of oak at first and then passes through the petiole and into the leaf-blade. Two species, *H. sericiella* and *H. resplendella* first mine down the midrib of a leaf and then turn up the edge of the leaf and make a blotch mine. In these instances the blotch is hardly more than big enough to make the case. They pupate in their cases on the ground.

Antispila

Members of this genus show a marked preference for host plants of the vine and dogwood families. The mines are blotched from the beginning. The larvae have been observed to plot out their cases first by covering with silk an oval patch of the floor and then a counter-placed oval patch of the ceiling of the mine. The larva cuts the pieces out by swinging the head from side to side, first depressed and then elevated. The convex edges are brought together and sewed with only a few moorings of silk to keep the case on the leaf until all is ready. Dropping with the case to the ground, they either remain on the surface or penetrate with the case a very short way into the soil for pupation. The shape of the case varies slightly with the species.

The larvae are slightly broader and flatter than in the other genera of this family. The head is strongly depressed and the front extends to the vertical angle.

Several species of Antispila mine the leaves of grape. One of these *A. viticordifoliella* is figured.

The sour gum case-cutter, *A. nyssaefoliella,* first makes linear mines which end in a blotch that often is widened so as to obliterate the earlier portion. It is widely distributed and very often destructive in the eastern United States.

Coptodisca

In this genus the mines are wont to begin as very narrow lines, afterwards expanding to a small transparent blotch.

FIG. 47

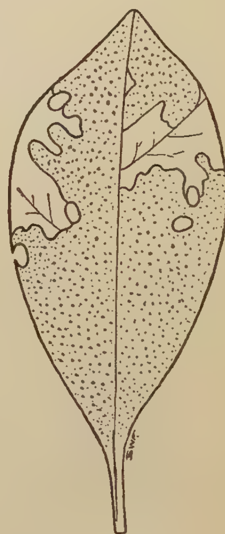


FIG. 48

FIG. 47. A leaf of wild grape bearing a mine of *Antispila viticordifoliella.*
FIG. 48. A leaf of sour gum bearing mines and excisions of *Antispila nyssaefoliella.*

The whole mine indeed is very small. Frequently there are many mines in one leaf. Busck has reported 30 to 40 mines in a single leaf for *C. arbutiella* and Comstock figures more than thirty mines of *C. splendoriferella* in a single apple leaf. While the cases of *Antispila* are usually cut from the very edge of its large blotch mines, the cases of Coptodisca

are usually taken from the geometrical center of the small blotches which terminate their mines. The leaves which have been infested by Coptodisca often look as though they had been clipped with a punch. The cases are let down by threads of silk and before pupation they are fastened down with a button or knot of silk. There is a record of an infestation of *C. splendoriferella* in which there were so many cut-out cases that the whole surface of a fence was plastered thickly with them. The larvae are somewhat fitted to drag their cases by reason of the sucker-like discs on the thorax. The anal prolegs, too, are represented by small lobes each with a small hook used in clinging to the case.

The resplendent case-cutter, *Coptodisca splendoriferella*, of the apple is a golden-headed mothlet (expanse 4.5 mm.) whose fore wings are of a lustrous leaden gray in the basal half, and golden, with silvery and brownish streaks beyond. Its habits were brilliantly described by Professor J. H. Comstock in his first report as Entomologist of the United States Department of Agriculture from which we quote as follows:

During the month of May, after the apple leaves have attained a sufficient size, I have watched the brilliant little adult of this insect running about upon the upper surface of the leaves in the bright sunlight with their wings folded close along their sides. I have never seen them deposit their eggs, and this is probably done at night. Neither have I ever been able to find their unhatched eggs, though the shells are plainly observable on the upper side of the leaf after the mine is sufficiently far advanced to show one where to look for them.

The young larva, hatching, penetrates to the interior of the leaf and begins a linear mine, which as it increases in size becomes an irregular blotch obliterating the earlier linear portion. This nearly completed mine bears a slight resemblance to that of *Tischeria malifoliella*, which is frequently found upon the same

leaf, but differs in the fact that the mine of the latter is only observable from the upper side of the leaf, while that of our insect can be seen from both sides and is also of a darker color.

The mine when completed is an irregular, frequently more or less triangular, rather dark colored blotch, averaging 6 or 7 mm. in its longest diameter and observable from both surfaces of the leaf. Up to the time when the larva has attained full growth, the mine is translucent, the only dark spots being the larva itself and the excrement which is collected in an irregular cake of minute pellets in the region where the mine was first begun. Soon, however, the translucency of the broader end of the mine begins to be obscured in an oval spot, and if it could be opened the larva would be found busily engaged in lining both surfaces of the leaf with white silk, mapping out the size and shape of its future case. After this lining has become sufficiently thick, the larva commences to cut through both surfaces of the leaf at the edge of the oval lining, and to draw them together and fasten them with silk as it goes. When the circumference of the oval has been cut and fastened, with the exception of a small portion at one end, the larva at that point cuts through the *upper* surface alone, partly issues from its case, and weaves a strong cord of silk from the surface of the leaf on beyond the mine back to the mouth of the case. Then, everything being securely fastened, it cuts the last band of the lower membrane which still remains intact, and stands upon the upper surface of the leaf with its completed case upon its back. The next step is to cut the supporting cord, and the larva is free to start upon its travels.

In walking, the head and first three thoracic segments alone are protruded from the case, the soft hinder parts being thus protected. The abdomen with the inclosing case is lifted erect in the air, so that it does not drag upon the insect as it walks. After progressing for an inch or so the larva usually drops from the leaf, spinning a long silken thread as it falls. In this way it either reaches the ground, or, what is much more common, falls upon or is blown by the wind to a limb or the trunk. It travels a greater or less distance further until it finds what seems to it to be a proper place, and there, after attaching the case firmly to the bark by a button of silk, it sooner or later transforms to a pupa.

No food is taken after the case is begun, neither is any excrement to be found in the case, all having been left behind in the mine. After fastening its case permanently, but before transforming to the pupa state, the larva reverses its position in the case, so that its head is towards what was formerly the posterior end.

When the time arrives for the moth to make its exit, the pupa works its way out through the posterior slit in the case until it is half emerged, and in that position gives forth the moth.

The individuals of the first brood transform to pupae almost immediately upon permanently fastening their cases, but the members of the last brood hibernate in the larva state [see pl. 2, fig. 6]. A case opened at any time during the winter will be found to contain a short, thick, yellow larva differing considerably from the mining form. . . . . In this state the insect remains until some time in March or April, depending upon the severity of the season, when it transforms to the dusky yellow pupa. The moth issues a week or so after the pupa is formed.

CHAPTER IX

Superfamily Gelechoidea

GELECHIIDAE

In this large family there are comparatively few leaf-miners, and these few are mostly single species in genera that are mainly of other larval habits. None of the miners are highly specialized for this sort of life. They are border-line forms, leaf-mining being mixed with other habits.

In the typical genus Gelechia occurs the aberrant miner already mentioned in Chapter I at page 28. There is also a European miner, *G. petastites* (of doubtful occurrence in North America). The following genera contain our better known species.

Phthorimaea

Two species of this genus mine in the leaves of Solanaceae. Best known is the tobacco split-worm, *P. operculella*, whose common name graphically describes the work of a generalized leaf-miner: it splits the leaf by removal of the mesophyll. This species is of world-wide distribution in tobacco-growing districts. It has proved a serious pest in parts of Florida, Tennessee and California.

Being something of an opportunist, it is also betimes a borer in tubers. In this rôle (with which we are not here concerned) it is known to the growers as the "potato tuber moth." The best account of its leaf-mining habits is that of Morgan and Crumb (14) from which we quote as follows:

> In forming its mine the larva begins by spinning a tent of silk between the mid-rib, or between the vein and the surface of the leaf. Under this protection it soon forms a shelter between the

leaf surfaces by consuming the parenchyma. The mined leaf becomes more or less distorted. Only the older tobacco leaves are affected, unless the infestation is very severe; and in these grayish, irregular blotches are produced, which later turn brown and become fragile, so that the tobacco is unfit for wrappers.

The egg is pale, translucent, yellowish gray, and strongly iridescent; it is oval, 0.45 mm. long, 0.35 mm. broad at the middle, membranous, and without apparent sculpture. The side upon which it is deposited is slightly flattened. Eggs are deposited singly upon the foliage of the host plant. Moths begin to oviposit two or three days after emergence and continue ovipositing for several nights. The largest number of eggs obtained from a

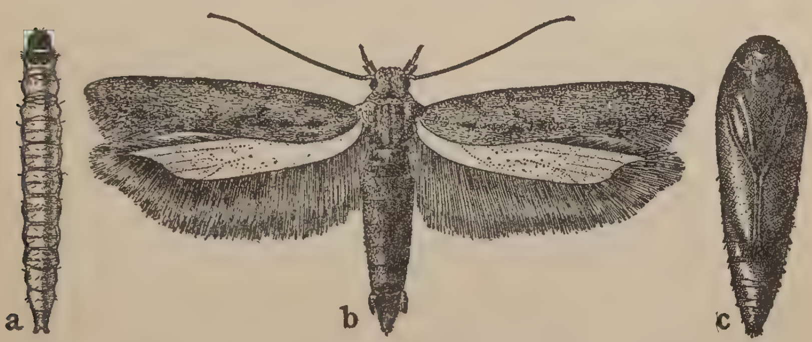


FIG. 49. The tobacco "split-worm" *Phthorimea operculella*. *a*, larva; *b*, adult moth; *c*, pupa.

single moth was 46, but this probably does not represent the maximum oviposition under normal conditions.

The full-grown larva is 7 to 14 mm. long. The head shield is 0.80 to 0.86 mm. broad and fuscous brown. The cervical shield is darker brownish fuscous, with a pale mid-dorsal line, shining, the posterior margin medially straight. The anal shield is brown. The mesothorax and metathorax are deep maroon. The body varies in color through green and gray and is overlaid dorsally with purplish as the larva nears pupation. The larva is very active, is capable of prolonged exertion immediately after hatching, and clings very tenaciously to the foliage. The frass is either stored in a particular part of the mine or is cast outside. The

larva pupates in a slight but somewhat tough cocoon of silk and debris among clods or rubbish at or near the surface of the soil.

The pupa is yellowish brown, 5.5 to 7 mm. long and 1.5 to 2 mm. broad; it is broadest through the metathorax, tapering both anteriorly and posteriorly. The abdomen, excepting the last three segments, is set with very minute spinules; it bears at the tip mid-dorsally a short, curved, erect, pointed horn flanked by about four pairs of long hooked spinules. Each abominal segment is set with a transverse row of spinules near the anterior margin.

The moth is slender, inconspicuous, with dark grayish wings bearing indefinite yellowish streaks and having an expanse of about 20 mm.

At Clarksville, Tennessee, the splitworm requires 25 to 30 days in summer for completing its development from egg to adult. Of this time 4 are spent in the egg stage, 15 to 17 in the larval stage and 6 to 9 days in the pupal stage.

The egg-plant leaf-miner, *P. glochinella*, is another species of this genus that mines the leaves of some of the same kinds of plants. It is distinguished by its habit of constructing within the mine a dense silken frass-covered tube. Jones (23) says:

The mines in egg-plant and *Solanum carolinense* are always along the edge of the leaf. A number of larvae sometimes work in a single leaf and at least two have been found using what were apparently parts of the same mine. The mined portion of the leaf has the appearance of a dry, oftentimes puffy blotch, the older mined area being dead and brown. The leaf becomes distorted about the mine and sometimes curls over it, but no silk is apparent on the leaf surface. The larva removes the parenchyma and constructs a firm silken tube, in which it is often found, within the mined area.

In its larval habits *Phthorimaea glochinella* apparently differs from *P. operculella* in that it feeds entirely within the leaf, not leaving the mine to roll the leaf or feed on other portions of the plant. The fact that the mines seem invariably to be made along the edge of the leaf is also a habit not shown by *operculella*.

Gnorimoschema

One species of this large genus is known to be a leaf-miner. It is a bit remarkable for the manner in which it combines leaf-mining with tube building. Chambers (1873) has told all we know about it. We quote him as follows:

> It constructs a case or tube of silk lined externally with its frass. The tube is nearly flat, but curved, one side being convex and the other concave, and it is wider at one end than at the other, and attached at its narrower end to the under surface of the leaves, and from it the larva passes into the leaf to feed, retiring into the case when alarmed, and to pupate. It constructs but one case, and I think the attachment of that one to the leaf is permanent, and that the larva makes but one mine. It mines the leaves of the skull-cap, *Scutellaria latifolia.*
>
> I have never found it except in a single locality—near the village of Verona, in Boone County, Kentucky. There it is very abundant in September and October.

The species appears to be extremely local. It is still known only from the one locality from which it was reported by Chambers more than fifty years ago.

Paralechia

Our knowledge of the habits of a single species of this genus, *P. pinifoliella,* we derive from Professor J. H. Comstock's first report (1879) as Entomologist of the United States Department of Agriculture. The larva is a miner in the pines that have leaves of the thicker sorts, pitch pine, scrub pine, etc. From his account of it, we quote as follows:

> The end of the leaf, and in many cases the entire leaf above its base, becomes dead and brown, and when opened it is found to be entirely eaten out, and to contain, in the proper season, the larva or pupa of the above-mentioned insect.

The larva, from a study of the mines, appears to burrow towards the end of the leaf first. Should it arrive at the end of the leaf (and it almost invariably does), before attaining full growth, it reverses its position and mines towards the base. The hole of entrance and of future exit is apparently in all cases enlarged and the excrement pushed through, as there is but little frass to be discovered in the mine, while it can always be found in a greater or less quantity at the opening or on the leaves below. No instance has been observed in which one larva has injured more than a single leaf of *P. rigida,* but a specimen of this insect was found in Virginia upon the common scrub-pine (*P. inops*), the leaves of which are shorter and more slender than those of the pitch-pine, and, from observations made upon it, it would seem that one leaf, if small, does not afford all of the food needed by a larva.

Upon reaching full growth the larva spins a slight covering to the mouth of the mine and retreats a short distance above it (from 10 to 15 mm.). There, after spinning a few supporting lines of silk, it transforms to a long and slender chrysalis, light-brown at first but afterwards nearly black. When removed from the mine the pupa is very active, jerking the short end of the abdomen (which extends below the wing cases) from side to side with rapidity. The duration of the pupa state is from ten to fourteen days. The moth makes its exit from the pupa shell without disturbing the position of the latter, leaving it attached by its threads some distance up the mine, and works its own way to the entrance.

There are certainly two broods of this insect each year, probably three, and possibly more in exceptional seasons.

Aristotelia

The three native species of this genus of which published accounts are available are so different in habits that we cannot generalize, but can only quote the brief notes on one of them.

Concerning *A. physaliella,* Clemens (1872) stated:

The larva mines the leaves of the "Ground Cherry (*Physalis vicosa*) in September, and perhaps earlier, as I found then many

empty mines. It mines the under surface, and produces a tubicular swelling of the upper surface. It pupates among leaves on the ground, and (in the breeding cage at least) the imago conceals itself among the leaves and "trash" on the ground. I have never seen any specimens except the two that I succeeded in rearing; but the mines are abundant. The following are my notes about the larvae: "Larvae now (October 6th) about $\frac{1}{4}$ inch long; one of these in the mine appears bright bluish-green, with the head yellowish; another is pale bluish or bluish-green, almost white, suffused with pink upon the back, head pale brownish. October 7th, one of them has left the mine; it is $\frac{1}{4}$ inch long, robust, deep purple, with the head and 'shield' of the first segment green. Two imagines, April 14."

Miss Braun added:

The species is by no means common. I have reared a small series of specimens from larvae collected May 28 in Powell County, Kentucky, on young plants of an undetermined species of Physalis. The leaves of this plant are thin in texture, and the character of the mine is different from that described by Chambers in leaves of *Physalis viscosa*. The mines are at first linear and contorted, later blotch-like, with most of the leaf substance consumed.

These records are both from Kentucky.

Chrysopora

Our two species of this genus mine the leaves of members of the goose-foot family *Chenopodium* and *Atriplex*. A good description of the larva and mine of one of them was given by Chambers (1872) as follows:

I have found it mining the leaves of species of *Chenopodium* in Kentucky and Wisconsin. The larva, at first, is white; but towards maturity, eight crimson spots make their appearance on each segment; four on top and two on each side. (Stainton says four, but in all of my specimens there are eight.) Sometimes some of the spots are confluent. It enters the leaf from the upper surface, and frequently leaves an old mine to construct a new one.

Frequently the leaves are scarred or blotched by numerous mines, and sometimes the whole leaf is mined, but in such cases there are several larvae in a mine. The typical form of the mine seems to begin as a point, from which it passes, gradually widening, first to one side, then to the other, in a series of loops, each extending a little farther than the preceding, like a band gradually widening, wound around a cone. The frass is scattered through the mine.

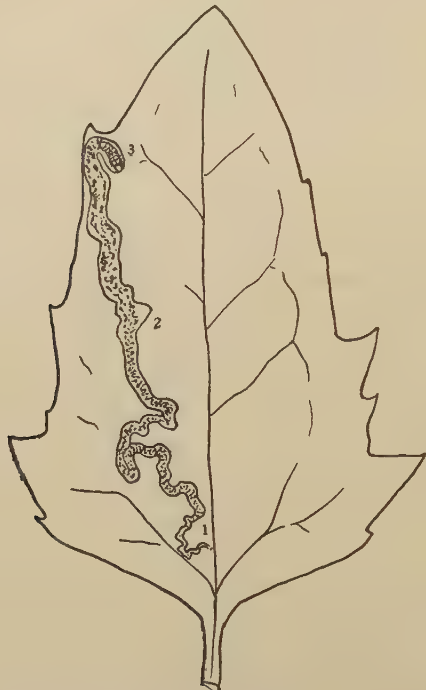


Fig. 50. A leaf of lamb's quarters bearing a mine of Chrysopora.

Such mines are common at Ithaca, New York, in goose-foot leaves in autumn. The accompanying figure of an unusually extended mine shows at *1*, *2* and *3* successive enlargements following successive moultings of the larva.

Recurvaria

This is a genus of minute moths whose larvae feed from shelters of various sorts. A few species are leaf miners; and these few show considerable diversity of habits. They infest both coniferous and deciduous shrubs and trees. In long-leaved conifers, like pines, the larvae work within the needles; in short-leaved ones, like arborvitae, they mine the leaf spray as a whole.

The pine leaf-miner of the Rocky Mountains, *R. pinella*, has been reported upon by Gillette (1922), from whose account we quote as follows:

It was easy to notice the brown foliage of the yellow pines at a distance of at least two miles. Upon examining the needles it was discovered that they were being mined by some small lepidopterous larva, which was present in very large numbers. The larvae usually enters the needle beyond the middle, making a very small hole. It feeds upon the pulpy interior until fully grown, when the needle may be almost completely mined. It then returns to a point just a little below the entrance and the exit apertures are closed with silk, the latter in a manner to direct the chrysalis out of this opening as it wriggles to it when the moth is ready to emerge. The chrysalis stage is passed within the mined needle near the bottom of the burrow.

The spruce leaf-miner, *R. picaella*, according to Gillette (1922), as already mentioned in Chapter II (p. 37) similarly mines the Colorado blue spruce, but differs in its mining habits as follows:

Unlike *R. pinella*, this species enlarges the entrance puncture and uses it mainly for the escape of the moth, pupation always being in the mined needles. *R. pinella* always makes its exit opening near to but a little below the entrance puncture and neither of these openings are very near the tip of the needle, while in this species, the entrance and exit opening is seldom more than one-eighth of an inch below the point of the needle.

This species is unique among leaf miners as it requires two years for its development.

The arborvitae leaf-miner, *R. thujaella,* is one that works in leaf-sprays (see pl. 2, fig. 5). It lays its eggs in a depression between two of the close-laid scale-like leaves. The larva on hatching crawls under the edge, and in the axil begins eating its way into the leaf. When it has eaten the mesophyll of one leaf, it enters another either through the base or through overlapping surfaces, without coming out into the open. Thus it extends its operations until a considerable portion of the spray is hollowed out, and appears transparent when held up to the light. The species hibernates as a larva, and pupation occurs in the mine. A good account of the species is given by Britton and Zappe (1922) with figures and bibliography.

The Ceanothus miner, *R. Ceanothiella* of the mountain region of central California, is a deciduous shrub-miner whose work has been briefly described by Miss Braun (1921) as follows:

> The mine starts on the lower side of the leaf, usually next the midrib; the entrance guarded by a short tube of silk. The mine is at first linear, with branches extending out from it, later, blotch-like, including the linear portion. Pupa in a cocoon between two leaves tightly spun together.

Nealyda

This genus includes a few southern and western species whose larvae are considerably flattened and whose pupae are formed outside the mine on a leaf in dense oval, flattened, white cocoons, from which the pupal skin is not protruded on emergence of the adult. The egg is laid on the upper side of the leaf. The mine is more or less trumpet form or blotched, having something of the appearance of Lithocolletis, as does also the flat larva, if one disregard legs and mouth parts. Two species from Florida and one from Colo-

rado are described by Busck (1901 and 1903). His description of the larva of *N. pisoniae* from Palm Beach, Florida, is as follows:

> The larva is, when full grown, cylindrical, somewhat flattened, strongly segmented, and tapering backward, about 7 mm. long. It has three pairs of normal thoracic feet, four pairs of abdominal feet suggesting the toes of a tree frog, being very long and thin with a globular swelling at the end; while in the mine they are pointed backward, flat to the body; no anal legs. Larva is white with light-brown head and thoracic plate; sutures in head darker brown. When mature it cuts its way out of the mine and spins nearby on the leaf a tough, oval, flat, white cocoon, from which the pupa does not protrude, when imago issues.

LAVERNIDAE

This is another family of minute moths in which the larvae commonly feed from shelters of some sort and a considerable portion of which are leaf-miners. Our representatives of the three following genera are all leaf-miners.

Psacophora

The larvae are rather generalized tissue feeders, somewhat depressed in form and with rather deep incisions between the body segments. Thoracic legs are well developed but prolegs are very small. They feed entirely within the mine but pupate outside. The work of *P. argentimaculella* was described by Miss Murtfeldt (1900) as follows:

> Mines leaves of *Oenothera biennis*. The mine begins in a winding tract, which crosses back and forth, often becoming confluent. The dark, granular frass forms a rather definite line through the middle.
>
> When ready to transform, the larva deserts the mine and incloses itself in a dense, oval, white silk cocoon formed against the midrib or in a wrinkle of the leaf. Pupa dark brown. Imago appears in nine or ten days.

Chrysopeleia

Our two northern species of this genus mine the leaves of the hop hornbeam. The best available account of the mining habits of one of them, *C. ostryaella*, is the old one by Clemens sent in a letter to Stainton in 1859 and published by the latter (1872) which we reproduce herewith.

I send you a leaf of *Ostrya virginica*, containing what to me is a novel mine. I found it for the first time a few days ago, when looking for cocoons intended for you. I should be glad to learn whether you know of any larva having a similar habit. The mine begins along the midrib, and scarcely ever exceeds the limit of the two veins, between which it is first commenced. Its peculiarity consists in the construction of lateral walls of "frass" within the mine, that are extended as the mine increases in length, forming a tube, transparent above and below, which leads to an opaque one alongside of the midrib of the leaf. When the larva is alarmed or disturbed it retreats along this way and conceals itself under the opaque portion along the midrib. It quits the leaf to transform, and weaves a little ovoid cocoon.

Cosmopteryx

We introduce this genus of dainty leaf-mining mothlets with Busck's (1906) brilliant description of them:

The little moths belonging to the genus *Cosmopteryx* are probably familiar to anyone who has collected and observed insects in nature. Who has not occasionally on a warm midsummer day met with a slender little streak of gold and silver sitting in the sunshine on a leaf in a protected corner and twirling its long white-tipped antennae in graceful motions? If, when examined very closely, it is found to be a smooth shining little moth, brown with silver lines on palpi and antennae, and with a striking broad golden or orange fascia across the outer half of the wing, bordered on both sides by bright metallic scales, then you have a *Cosmopteryx*.

Most of the species may at once be recognized by this characteristic ornamentation alone, without structural examination.

The larvae are leaf-miners, and the mines are easily distinguished from most others by the scrupulous cleanliness with which the larva ejects all its frass through a hole, so that the mine remains clear and white. At maturity the larva changes its color from green to a vivid purple or wine-red, leaves the mine, and spins a matted flattened cocoon of silk.

The larvae, as far as known, seem to prefer herbaceous plants—principally vines and grasses.

The rich-weed leaf-miner, *C. pulchrimella,* infests the leaves of *Pilea pumila,* "mining, twisting and crumpling

FIG. 51. A leaf of enchanter's nightshade bearing a mine of Cosmopteryx.

them." The larvae may leave the mine and wander about over stems and leaves "cutting in between the two cuticles of a leaf, and covering it with transparent spots of various sizes."[1] Pupation is outside the mine in a fold of the leaf or on the ground "protected by a very slight dingy cocoon."

The work of a panic grass leaf-miner, *C. gemmiferella,* is described by Miss Braun (1923) as follows:

The larva mines the small basal leaves of *Panicum dichotomum* Linnaeus, in the spring, eating out almost the entire substance of the leaf. Just before pupation, it enters one of the lower stem leaves, in which it makes a small inconspicuous mine, scarcely

[1] From Miss Murtfeldt, as quoted by Busck (1906).

larger than the larva, but broadening at its anterior end toward the tip of the leaf, slightly inflated, and showing as a convexity on the upper surface of the leaf. Within this cavity, which is silk-lined, pupation takes place. Beyond the pupation chamber, the mine extends a short distance forwards, but is scarcely visible except at its end, where the epidermis is almost eaten through, permitting the emergence of the imago.

There is apparently but one generation a year; the moths appear from the latter part of May to July.

The work of another species, *C. clandestinella*, in a different species of panic grass, *P. clandestinum*, which differs in several minor points, as shown by Busck's (1906) description:

Mine with the frass ejected at one end. The larva is light green with short light hairs and with yellow head and thoracic shield. At maturity it assumes a brilliant wine-red color in three broad longitudinal stripes, and cuts a circular piece out of the epidermis of its mine, which it bends lengthwise and uses for a cocoon exactly like the genus *Cycloplasis* Clemens.

CHAPTER X

Superfamily Yponomeutoidea

YPONOMEUTIDAE

Of this rather large family only relatively few isolated species are known to be leaf-miners, and they are of a very unspecialized sort, with cylindric tissue-feeding larvae that pupate outside. The habits of the juniper miner, *Argyresthia annetella*, are summarized by Forbes (1923) as follows:

The larva mines about four leaves at the tip of a juniper twig, passing through the stem from leaf to leaf, completely emptying the leaves on scattering the frass. It hibernates in the mine; it pupates in May in a cocoon of open meshes formed outside.

The grass-mining Scythris, *S. graminivorella*, was reared by Miss Braun from leaves of Hystrix. She says:

The mine is an elongate transparent blotch with the entrance[1] guarded by a broad tube of silk; the larva usually *makes several mines*. Although the species seems to prefer *Hystrix* as a food plant, I have observed the mines on Canada blue grass, *Poa compressa*. Larvae collected May 5, produced moths during the first half of June.

Most members of the typical genus Yponomeuta (the ermine moths) do not mine at all; but at least one of them *Y. malinellus*, is a leaf miner during a part of its first instar.[2] Parrott and Schoene (1912) have given the best account of

[1] In *Hystrix*, the leaf blade is twisted near the base, so that the upper surface of the leaf faces downward.

[2] This species is singular in that the eggs are laid in masses on the twig of apple and the larvae must seek the foliage.

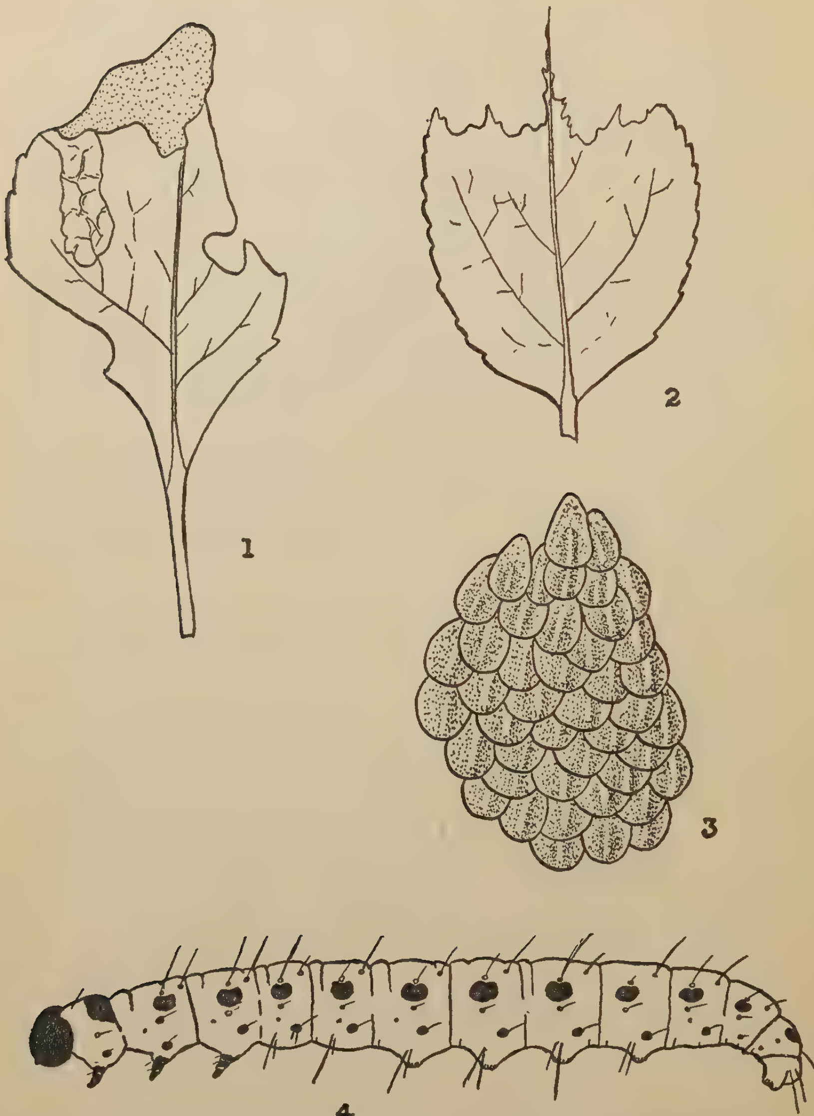


Fig. 52. *Yponomeuta malinella* drawn from Parrott and Schoene, Geneva Bull. 24, 1912. *1*, mined area on apple leaf; *2*, characteristic feeding of older larvae on apple; *3*, egg mass laid on twig; *4*, mature larva.

the habits of this species, whose larvae hatch in autumn and remain inactive until spring. Then the young caterpillars assemble among the tender leaflets of an opening apple bud and bore into the parenchyma "beginning at the edge usually near the apex of a leaf. As many as a dozen insects may exist as a colony within the pulpy substance of a single leaf. Within a few days after their entrance, the leaves turn reddish at the points of injury, and those more severely mined may wither and die. Toward the end of the time of blossoming, the caterpillars cease to burrow and feed openly on the leaves l. c., p. 62).

GLYPHIPTERYGIDAE

In this family but one of our northeastern species is reported to be a leaf-miner, and that one only when a young larva. It feeds on everlastings (Antennaria and Gnaphalium in Compositae). It leaves the mine and thereafter lives "in a sticky web mixed with frass" (Forbes, 1923). A number of larvae gather together to spin their cocoons.

FAMILY HELIODINIDAE

In this family also a native species, *Cycloplasis panicifoliella*, is reported to be a leaf-miner. It feeds on *Panicum clandestinum*. Dr. Brackenridge Clemens thus describes its habits.

The larva makes at first a long, threadlike mine from the base of a grass leaf to its tip and then down along one side to about the middle of the leaf where it makes an irregular blotch. When it is full-fed it cuts out a case but this is made from a perfectly circular disc of the upper surface only of the mine. This disc it folds along the diameter, sewing the semicircular edges together from the inside. Case and larva then fall to the ground where the larva attaches the case for pupation. It feeds in late June and early July and emerges as an adult by the end of the month.

A Rocky Mountain species of Litharapteryx, *L. abroniaella*, was reported by Dyar (1903) to be a leaf-miner of mixed habits:

> The larvae form variously shaped blotch mines, with a hole by which frass is extruded; they also spin among the terminal leaves or flower bracts with a delicate web in which the frass is contained. The food plant is *Alliona nyctaginea.*

An odd bit of very localized and temporary leaf-mining occurs in another member of this family, *Erineda aenea,* as reported by Miss Braun (1918):

> The larvae feed on the spores of two species of ferns (*Asplenium angustifolium* and *A. acrostichoides*). A web, beneath which the larva feeds, is spun along the under side of the leaflet, often extending for three-fourths its length by the time the larva reaches maturity. When young the larva mines into the sorus, eating out the greater portion of the spores, and leaving the indusium hollow. Later the larva becomes too large to mine, and consumes the entire sorus, except the annuli of the sporangia.

CHAPTER XI

SUPERFAMILIES TORTRICOIDEA, PYRALIDOIDEA AND NOCTUOIDEA

FAMILY TORTRICIDAE

In this great family, besides the tube-dweller, *Epinotia aceriella*, there are few species of known leaf-mining habits, though probably others will yet be found. One is *Epinotia heucherana*, whose larva lives in a digitate mine on the leaves of *Heuchera americana*, and is deep red in color, with a black head and prothoracic shield.

FAMILY PYRALIDAE

Of this immense group, one species of the eastern United States is an ordinary leaf-miner, one is an aquatic leaf-miner, and one very large species, *Melitara prodenialis* (already mentioned in Chapter I at page 26) is a gregarious miner in the phyllodia of cacti.

The sunflower leaf-miner, *Autocosmia helianthales*, as a larva forms large blotch mines in the leaves. It is pale green in color, with a rosy tint. The head is whitish in front and mottled with brown above. Two large brown spots cover most of the prothoracic shield. The frass is scattered mostly on one side of the mine. The pupa is usually formed in the mine. There are three broods and the last hibernates in the larval stage within the cocoon.

One undetermined species of the aquatic genus Nymphula, having a larva with reduced gills, has been found by Dr. W. T. M. Forbes in its earliest instar mining the leaves of water lilies.

FAMILY NOCTUIDAE

Of this enormous family a very few species are leaf-miners and these only for a little time while they are small. They soon grow to a size quite too large for the space between the upper and the nether epidermis of a leaf and turn to other habits. It is probable that among the many smaller noctuids, the larval habits of which are unknown, other leaf-miners will yet be found.

Those at present known in our region belong in the allied genera Bellura, Sphida, Arzama and Nonagria, their larvae are rather ordinary tissue-feeding caterpillars of extraordinary habits. We will select two of them that have been carefully studied in this country for illustration.

The cat-tail Arzama, *Arzama obliqua*, is a miner during its first larval instar in the leaves of *Typha latifolia.* These leaves are divided lengthwise by a series of IIIII-like partitions between upper and lower cuticles, forming long channeled interspaces between the I's, and these channels are crossed by thin partitions of parenchyma cells. These channels are the home of first instar larvae and the cross partitions are their food. From the excellent account of Dr. P. W. Claassen (1921) we condense the following:

The eggs are laid on the surface of one of the first-formed leaves of *T. latifolia,* from 6 to 15 inches below the tip. The egg mass is covered with a thick layer composed of a mixture of froth, hairs, and scales from the body of the female. The egg mass resembles a mass of spider's eggs. It is of a dirty yellowish-white color. It measures from 12 to 15 mm. in length, from 7 to 10 mm. in width, and from 3 to 4 mm. in height at the center. In shape it is oblong and convex, the edges gradually thinning out and adhering closely to the surface of the leaf. The long axis of the egg mass corresponds to the long axis of the leaf. Without devouring the egg shell, the embryo breaks through it and bores directly into the leaf of the cat-tail where it works as a leaf-miner. Once the larvae enter the leaf, they begin

their work as leaf-miners. They begin to mine, mostly downward, scraping off the chlorophyll from the upper and lower epidermis of the leaf. They eat out the transverse partitions, leaving the longitudinal partitions and the fibro-vascular bundles undisturbed except when occasional larvae cut through to get in other channels.

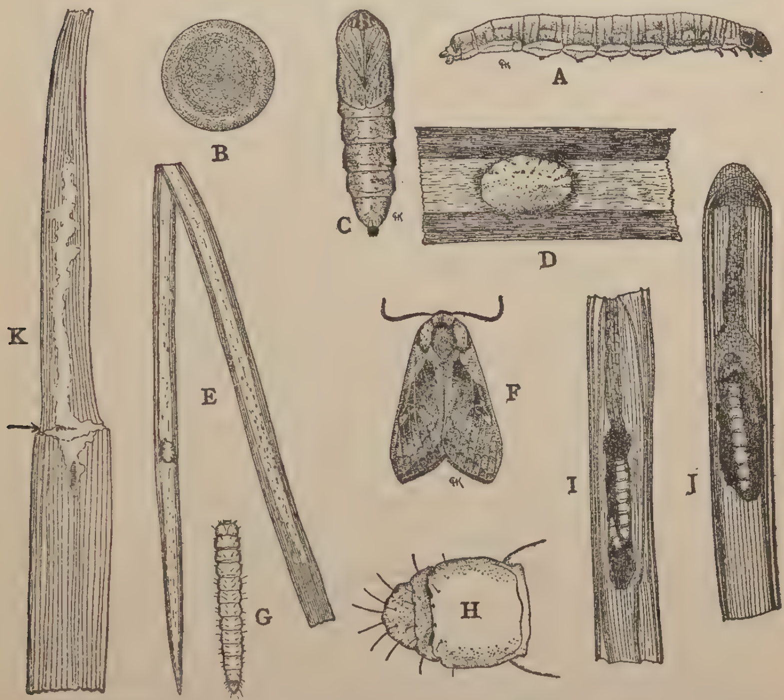


FIG. 53. The life history and work of *Arzama obliqua*. (After Claassen.) *A*, larva; *B*, egg removed from cluster and highly magnified; *C*, pupa; *D*, egg cluster; *E*, a leaf of cattail showing at the left the egg cluster where the miners enter, and at the right their exit holes; *F*, adult moth; *G*, young larva; *H*, last larval segments from above; *I* and *J*, older larvae as stem borers; *K*, the mining operations of another Noctuid larva, *Nonagria oblonga*.

A few of the larvae may first mine upward toward the tip of the leaf, but soon they all proceed downward, moving abreast along the channels. After the larvae have mined down for a distance of 20 to 24 inches, they molt in the mines and immediately afterward leave the mines through a little exit hole which is usually

made on the inner side of the leaf. As soon as the larvae appear on the surface of the leaf they at once seek shelter, usually continuing down the stem of the plant and crawling behind the sheath of one of the outer leaves. They later become stem borers.

Claassen in the same paper (1921) gives an account of another related cat-tail borer, *Nonagria oblonga,* whose larvae are miners through two or three instars, making irregular mines that traverse the I-like partitions and flex and kill the leaf tips.

The spatter-dock leaf-miner, *Bellura melanopyga,* is a miner first in the leaf blades and later in the leaf stalks of *Nymphaea americana.* From the excellent and detailed account of its habits given by Welch (1914), we condense the following:

Two fairly well defined periods can be recognized, the *mining period,* which lasts approximately throughout the first two stadia, and the *petiole period,* which includes the remainder of the larval existence. During the mining period the larva works on the upper side of the leaf. It usually cuts a somewhat circular hole, slightly larger than itself, through the upper epidermis and penetrates into the parenchyma. There is no regularity in the shape of the mine. Sometimes it appears as a winding tunnel with a diameter about twice that of the larva; sometimes it is digitate in appearance, and sometimes it resembles a blotch mine. Holes through the epidermis other than the original entrance may occur anywhere throughout the length of the mine. Mines are easily detected on the surface of a leaf since they soon become whitish in appearance, due to the removal of the chlorophyll-bearing tissue. The inital entrance to a mine is usually surrounded by excrement and a small quantity of finely masticated leaf tissue.

Even in the very early stages the larvae are active feeders. Larvae, 5.5 mm. long, constructed mines 14 mm. long in less than 20 hours. Larvae, 7 mm. long, when transferred

to new lily leaves completely buried themselves in four hours. Usually but one larva occupies a mine. Several instances were observed, however, in which two were occupying the same mine and in one heavily infested leaf eight larvae of about the same size were found in a single, large mine. The formation of the mine is due primarily to the fact that the larva apparently uses only the parenchyma as food and must get under the epidermis in order to get it.

Several days after the mine has been formed the upper and lower epidermis bounding it begin to disintegrate, ultimately leaving an ugly hole in the leaf and, in badly infested leaves, producing numerous perforations. The effect on the plant is evident. Not only is the leaf disfigured but in proportion to the number of holes present the leaf surface is also reduced. Many cases were observed in which the infestation was great enough to cause the death of the entire leaf.

By the end of the second instar the larvae are too large to continue as miners in the leaf blade. They then travel to the midrib, often to the base of it, either openly creeping upon the surface, or cutting slits as they go through the leaf tissue; they bore into it, always downward, and thence down the petiole. The length of the burrow in the petiole varies according to the time it has been inhabited, and to some extent according to the size of the larva. Burrows were frequently two feet long and occasionally longer.

In the field the best mark of recognition of the work of these larvae is the heap of excrement which accumulates around the margin of the burrow on the upper side of the leaf. As would be expected the quantity depends upon the length of occupancy and the activity of the larva. In August it was a common thing to find hundreds of leaves with conspicuous heaps of excreta around the hole on the upper surface. The excrement is always deposited outside of the burrow.

During the leaf-feeding period respiration is carried on in the same way as in terrestrial lepidopterous larvae. Each larva is working in a mine in the leaf but the entrance hole and other openings which usually occur are sufficient to provide the necessary air. When the larva deserts the leaf and becomes a borer in the petiole new conditions are encountered and new provisions must be made. The burrow in the petiole is filled with water and the larva is submerged. When the length of the burrow increases to such an extent that it is longer than the body of the larva which is making it, the latter makes periodic trips to the surface where the fresh air is drawn into the tracheal system in sufficient quantity to allow a sojourn of several minutes under water at the bottom of the burrow. When at the bottom of the burrow the larva feeds (or in some cases merely rests) until the need for air stimulates it to return to the surface. Then it *backs up* to the top of the burrow, stopping when the large pair of posterior spiracles is just pushed above the surface film. It remains in that position until sufficient air has been taken into the trachea to permit a return to the bottom of the burrow again. This alternate sequence of feeding and breathing goes on continuously so long as the larve remains in the burrow.

CHAPTER XII

Order Coleoptera

Comparatively few beetles have developed leaf-mining habits. These few are members of three different and widely separated families, in each of which the habit has probably developed independently. In degree of specialization, none of the mining grubs are so greatly modified as are the sap-feeding leaf-mining caterpillars. Though some of them resemble these sap-feeders in general shape, all of the leaf-mining grubs are tissue feeders.

In the family Buprestidae, wood-boring is the predominating habit. The Chrysomelidae are mainly leaf-eating beetles that feed openly. The Curculionidae tend strongly toward seed-eating. Different as are the adults in these families the leaf-mining larvae look much alike. They show marked convergence in form. All are somewhat flattened, and have more or less wedge-shaped heads, that taper forward to the jaws.

The table on page 182[1] will show the distribution of leaf-mining habits in this great order.

The Buprestid and Curculionid leaf-miners and one group of the Chrysomelid larvae, are legless. Most of the Chrysomelid larvae are depressed, but furnished with thoracic legs. The larvae of the mining weevils have no true legs, and are not greatly depressed, as a rule. Several of them have the abdominal segments rather arched above and crowned with a retractile area which apparently functions in progression much in the fashion of a proleg. The leaf-mining flea-beetles are slightly depressed and their thoracic legs are well developed. They

[1] Altered from Frost, 1924.

The Leaf-Mining Genera of Coleoptera §

FAMILY	GENUS	DISTRIBUTION	NUMBER OF DESCRIBED SPECIES	NUMBER OF LEAF-MINING SPECIES‡
Buprestidae	Trachys	S. A., Eur., Asia, Africa	350	6
	Brachys	N. A., Mex., C. A., S. A.	100	4
	Pachyschelus	N. A., C. A., Asia, Africa	164	4
	*Taphrocerus	N. A., C. A., S. A.	43	1
	*Lius	W. I., Mex., C. A., S. A.	75	0
	*Leiopleura	W. I., Mex., C. A., S. A.	85	0
	*Leiopleurella	Panama	1	0
	†Callimicra	Mex., C. A., S. A.	29	0
	†Aphanisticus	Eur., Java	29	1
Chrysomelidae	Zeugophora	N. A., Eur., Asia, Ceylon	19	5
	Monoxia		?	1
	†Phyllotreta	N. A., Eur., Siberia, N. Zealand	46	4
	*Hippuriphila	N. A., Europe	2	1
	Epitrix		?	1
	Mantura	Europe	?	1
	†Chaetocnema	N. A., C. A., S. A., Ind., Eyr., Sib.	107	1
	Mniophila	Europe, Ceylon	3	1
	Dibolia	N. A., S. A., Cuba, Eur.	36	3
	Microrhopala	N. A., S. A., C. A., Mex.	16	3
	Uroplata	N. A., S. A., C. A., Mex.	55	1
	Octotoma	N. A., S. A., C. A., Cuba	6	2
	Chalepus	N. A., S. A., C. A., Mex.	123	7
	Baliosus	N. A., S. A., C. A., Mex.	24	2
	†Bronthispa	S. A., Australia	6	1
	†Hispa	N. A., Eur., Asia, Africa	75	3
	†Hispella	Europe, Africa, Ceylon	6	1
	†Promecotheca	Asia, Aus.	15	1
Curculionidae	Orchestes	N. A., Eur., Siberia	58	21
	Prionomerus	N. A., S. A., C. A., Mex.	17	1
	Rhampus	Europe	4	4
	†Cionus	Europe	12	1
	†Brachyonx	Europe	2	1
	†Ceutorrynchus	Europe	?	1

*Probably all the species of these genera are leaf-miners.

† These genera are leaf-miners only in part.

‡ These are the number of leaf-mining species whose habits are well known.

§ Taken from Frost (1924).

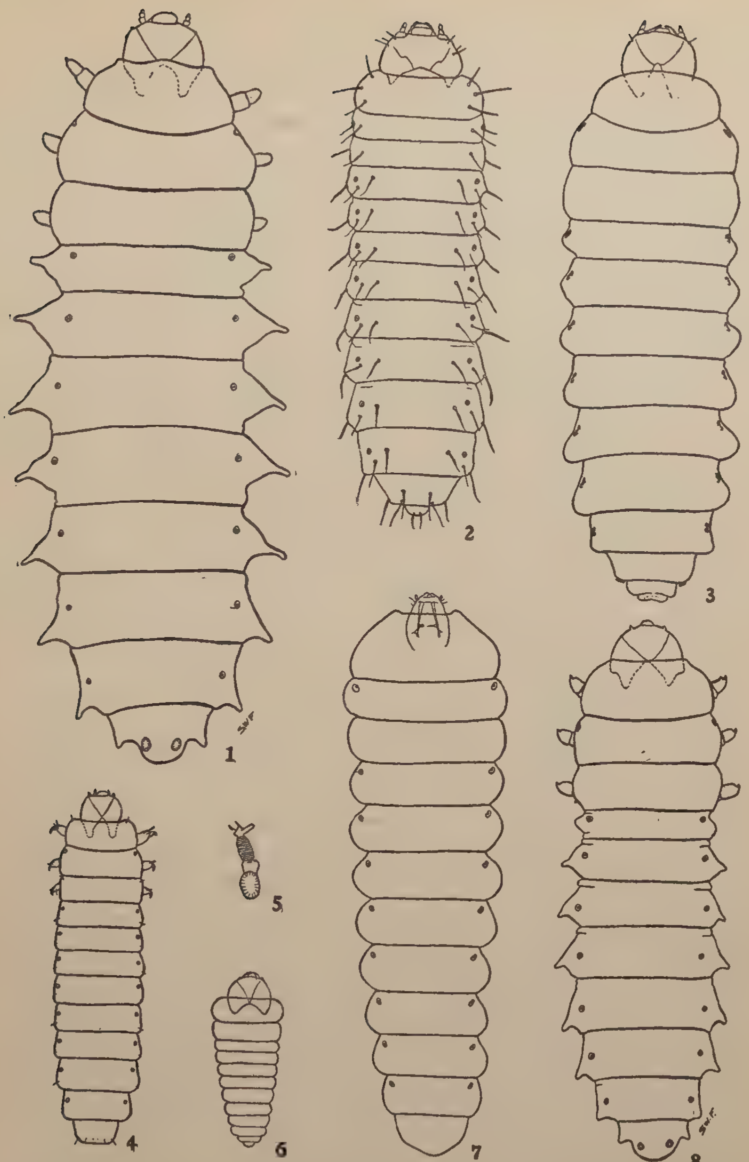


FIG. 54. Some larvae of leaf-mining beetles. *1, Chalepus scapularis; 2, Zeugophora scutellaris; 3, Octotoma plicatula; 4, Dibolia borealis; 5, Chalepus scapularis,* posterior spiracle; *6, Orchestes rufipes; 7, Brachys ovata; 8, Chalepus dorsalis.* Drawn by S. W. Prost.

are perhaps as little modified as any larvae of leaf-mining insects.

The eggs of nearly all of the leaf-mining beetles, except Curculionidae are laid upon the surface of the leaf. In several cases they are coated and protected with excrement. The eggs of the weevil leaf-miners are laid in the leaf tissue, the holes for them being first excavated by the beak of the females.

Many of the Chrysomelid grubs have the habit of deserting a mine in one leaf to migrate to another which they enter at a new place. The majority of them are active in the spring and early summer. The mines which they form are in many cases rather puffed or blistered.

With the exception of the few very generalized Chrysomelid larvae the beetle miners pupate in the mine and emerge from the leaf as adults. Some of the weevils have the rather distinctive habit of spinning in their mines a silken cocoon for pupation.

The adult beetles from these respective groups of mining grubs can be easily distinguished. The weevils will be recognized at once on account of having the head produced into a beak or snout. The Buprestids may be separated by their rather bronzed and metallic appearance and by the presence of grooves near the margin of the underside of the thorax for receiving the infolded antennae. The Hispid beetles are wedge-shaped with the hinder end broad and truncate. The surface is usually strongly pitted and reticulated in our American species and some exotic ones are even spiny. The front of the head is flexed so that the mouth is inferior. The flea beetles have a smooth often shining surface and a regular oval form. Their posterior thighs or femora are greatly thickened for jumping.

The relation of the leaf-mining habit to other habits in these various families is at first not very clear. Its existence in the Buprestidae where most of the species bore in the wood

seems anomalous. It must be remembered, however, that some of the wood borers work in the thin sheet of soft and juicy cambium tissue between hard wood and bark and that this limited environment is not very different from the thin layer of tissue in a leaf. In the case of the weevils the leaf-miners have perhaps been developed from the stem-dwellers through petiole borers and forms that live in the large ribs of leaves. The Chrysomelidae as a family are attached to leaves and it seems rather natural that some of

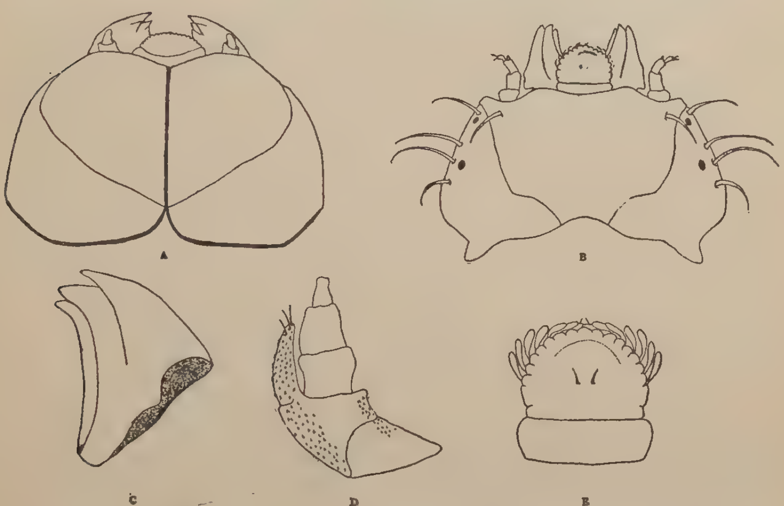


FIG. 55. Heads of two leaf mining beetles. *A*, Phyllotreta; *B*, Zeugophora; *C*, Mandible; *D*, Maxilla; *E*, Labrum.

the smaller ones should have sought protection by burrowing in leaf interiors.

The leaf-mining Coleoptera are particular in the selection of their host plants. They resemble the Lepidoptera and the Hymenoptera in this respect but differ from the Diptera which are, as a rule, general feeders. Brachys and Trachys have been found almost entirely on the woody plants, although there are European records of Trachys reared from mines on the leaves of *Malva rotundifolia*. Taphrocerus

mines Scirpus while Pachyschelus is a miner on Quercus, Lespedeza and Trifolium. The Curculionidae confine themselves to woody plants. The Chrysomelidae mine chiefly in herbaceous plants although Zeugophora and Chalepus occur for a large part as miners on the woody plants. Microrhopala is found entirely as a miner on asters and goldenrods.

The larvae of Coleopterous leaf-miners parallel those of Lepidoptera, without attaining quite so high a degree of specialization. The body becomes flattened, with bulging lateral expansions of the abdominal segments. The legs dwindle or disappear, and the head becomes wedge-shaped

FIG. 56. Heads of two mining leaf-beetle larvae. *A*, Chalepas; *B*, Zeugophora.

—depressed, with thin, flat mouthparts forming the front margin of the wedge. The mouth swings upward to a horizontal position and the frons extends to rearward between the side pieces of the epicrania. The latter are prolonged backward into the front of the prothorax where strong muscles attach to them. By means of these the head in feeding is moved up against fresh leaf tissue, while the body is held stationary on its paired supports. Thus movements of the head forward and backward (in and out of the front of the prothorax) guide the jaws into position favorable for food-getting. The accompanying drawings

Fig. 57. Types of Coleopterous leaf mines. *1*, mine of *Zeugophora abnormis* on poplar; *2*, mine of *Baliosus ruber* on apple, also showing the feeding scars of the adults; *3*, mine of *Dibolia borealis* on *Plantago major;* *4*, mine of *Phyllotreta nemorum* on seedling leaf Brassica, also showing the feeding scars of the adults (European); *5*, mine of Orchestes on apple, showing cocoon within the mine.

by Miss Helen Reed of the head of two little leaf-beetle miners show the differences in extension backward of the frons and of the hind angles of the epicrania, and the flattening and widening of the mouthparts that are the signs of progressive adaptation. Figure 56 shows greater backward extension of the frons.

The mines of the Coleoptera are chiefly of the blotch type. Often the mine is blister-like, making a large pocket within the leaf. Dibolia makes long tortuous mines which seldom become blotched except when many larvae are mining in the same leaf. Hippuriphila and Phyllotreta make short linear or serpentine mines while Orchestes starts as a linear mine but later changes to a blotch-mine.

FAMILY BUPRESTIDAE

In this great family of metallic wood-boring beetles, there are known leaf-mining members of five genera. About half a dozen species of the large European genus Trachys have long been known to be leaf-miners. One species of the Old World genus Aphanisticus, *A. consanguineus,* mines the leaves of sugar cane in Java. Several species of the cosmopolitan genus Pachyschelus are miners, but all are very insufficiently known. Certain species of Brachys, Pachyschelus and Taphrocerus, have been carefully studied in North America, and these will serve to illustrate the family. We select one that is a miner in leaves of oak, one in Desmodium and another in bulrush.

Life History

The egg. The eggs are laid singly upon the surface of a leaf. They are soft, and when covered with a transparent secretion that overspreads them, they settle down upon the surface in a low dome-shaped form. Often they are further covered and hidden by lumps of excrement. In hatching

the larva bores through the flat attached surface directly into the leaf.

The larva. The larvae are legless. When first hatched they are of the flattened "tadpole" shape characteristic of this family; only a bit flatter than usual. The prothorax is greatly widened, and behind it the body is rather suddenly contracted to parallel sides in the rear. The head is retracted into the first body segment. This segment is subquadrangular in shape, being wider than the remainder of the body and several times as long as any other segment. The median third of this segment is furnished with rectangular brownish plates on the upper and under sides. On the front border of this first segment at its sides are two little fleshy projections that in life are capable of considerable movement and that seem to aid in determining the direction of progress. There are fine backwardly directed setulae over the body, and there is a small spine on the anal segment: these are no doubt of great assistance in pushing forward.

There are three larval instars and after the first the larva becomes more elongated and a little less flattened. Broad, flat callosities are developed underneath the thoracic segments.

The larvae make blotch mines whose borders are more or less determined by principal veins. All the mesophyll is eaten out of them and the coarse frass is cast toward the center in irregular heaps, while the larvae feed in the clean, outer borders of the mine. Each moult occurs, and pupation as well, in the central spacious part of the mine.

The pupa. The naked pupa is strongly depressed in form and heavily chitinized. Often, in a puffy mine, it lies so loosely that it may rattle about like a pea in a pod. The appendages are rather closely sealed together and are immovable.

The adult. The leaf-mining Buprestids are, naturally,

among the smallest members of the family, but they are of the typical compact form and usually of shining metallic coloration. Antennae and legs fold so compactly in grooves that the ventral surface of the contracted beetle is almost as smooth as the dorsal. There is a single brood annually. Hibernation occurs in either pupal or adult stages.

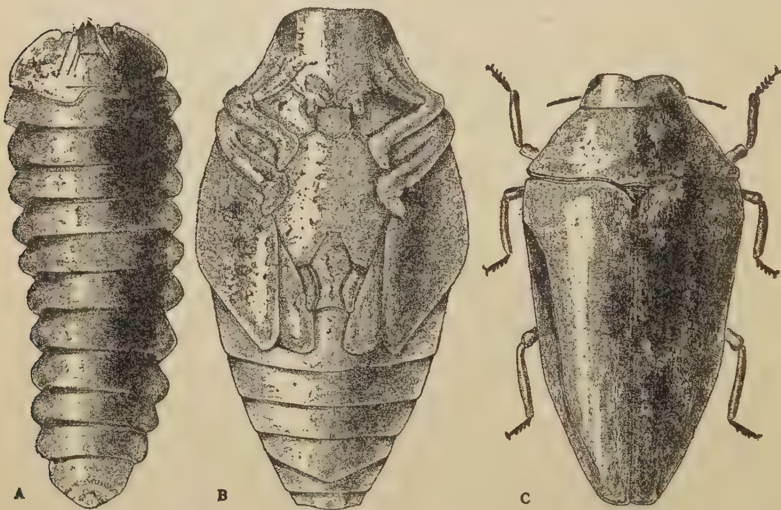


FIG. 58. *Brachys ovata.* (Drawings by Miss Ruth St. John.) *A*, larva; *B*, pupa; *C*, adult.

Brachys

The habits of most of the members of this large American genus are still unknown, but among them are four that are known to be leaf-miners. One of these, *B. ovata*, we have studied with some care. It is rather common at Ithaca, New York, in the leaves of red oak; less common in chestnut oak. It makes a rather large brown mine on one of the broader interspaces of the leaf, sometimes crossing the midribs. The mine is rather opaque, owing to the thickness of the leaf cuticle, but in the thinner, cleaner border portion

the shadowy outline of the feeding larva may be dimly seen, when held to the light. The flat, scale-like egg persists upon the surface when the mine is old, a shining speck that is easily seen when so held that the light is reflected from it.

A large number of rearings of larvae of this species were made by Miss Ruth St. John, at Ithaca, during the winter

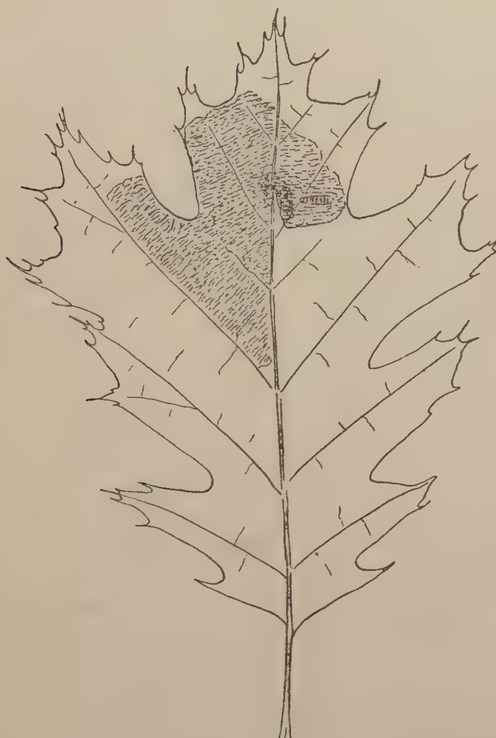


FIG. 59. Leaf of red oak with mine of *Brachys ovata.*

of 1924–1925, and she determined, contrary to published statements, that the winter is passed in the larval stage within the mines in the fallen leaves; that the pupae are formed in the latter part of the month of May (on May 13th the earliest was obtained out of doors); and that the pupal

stage is very short, averaging about 7 days. When the adult beetles emerge from their pupal skins they are at first white, and the hairs and scales do not yet show their metallic hues. Later comes the darkening and the development of iridescence. Her drawings are reproduced herewith.

Pachyschelus

The most careful study that has yet been made in this country of a member of this genus is that of Weiss and West (1922) from which we copy the following concerning *P. laevigatus*:

The eggs are inserted in a little pocket made usually in the lower surface near the edge of the leaf of Desmodium. The subcircular, nearly flat, jelly-like egg is deposited under a thin layer of tissue. Both the tissue above and below the egg are pushed out slightly and this results in somewhat flat, oval-like blister or swelling which is visible on both leaf surfaces. The tissue over the egg on the lower leaf surface becomes dry and whitish, 'while the upper surface of the blister becomes somewhat reddish.

The mine is started from the egg pocket and later extended in a somewhat irregular and linear manner. By the middle of July most of the larvae are nearly three-quarters grown and by the last of July many are full grown and the mines are completed. On the upper leaf surface the mines appear as dry, brown, irregularly linear areas. A few are blotch-like. The number of mines in a leaf varies from one to three, but is usually only one.

When the greenish larva is full grown it hollows out a circular cavity at the end of the mine. Such cavities are about 5 or 6 mm. in diameter. In this place it constructs a circular, somewhat flat, thin, tough, parchment-like cocoon about four millimeters in diameter. These cocoons push out the upper and lower leaf tissues somewhat into comparatively large blister-like swellings. By the first week of August all of the larvae are in these cocoons. At this time the tissue over the linear mines starts to break and this, together with the feeding which takes place earlier in the season, cause the leaves to turn entirely brown and start to curl up toward the midrib.

After the larve enters the cocoon it shrinks longitudinally into semiquiescent, compact, prepupal stage, in which it remains until the following spring, when it transforms to a pupa. The prepupal stage is long and lasts almost from the first of August until the following May. By the first week in September the cocoon with the dried leaf tissue over it somewhat resembles a *Desmodium* seed in color and shape. Later the leaves containing the cocoons and in fact all of the leaves fall to the ground and here the prepupa passes the winter.

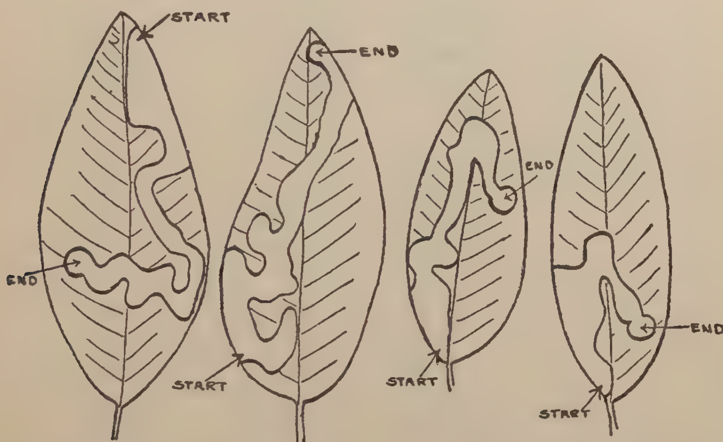


FIG. 60. Leaves of Desmodium with mines of *Pachyschelus laevigatus*. (From Weiss and West.)

Taphrocerus

One species, *T. gracilis*, has been carefully studied and reported upon by Chapman (1923). We borrow one of his figures, and abstract a portion of his account of its habits.

Its host plant is the flood-plain bulrush, *Scirpus fluviatilis*. About the end of June the eggs are laid singly on the surface of the fully developed leaves, almost anywhere from base to tip on either side but generally about midway between the midrib and a leaf margin. They are soft and translucent when laid. They flatten out on the leaf like a viscid drop-

let, the margins becoming very thin and the central mound about half a millimeter in thickness. A hardened, transparent, mucilaginous secretion glues each egg to the leaf.

The larva eats its way through the attached side of the egg directly into the leaf. The longitudinal ribs on the leaf surface are just far enough apart to allow the flat larva to pass between, and enter the mesophyl. There are three

FIG. 61. Leaf of *Scirpus fluviatilis* with mine of *Taphrocerus gracilis*. *A*, upper; *B*, lower side; *e*, egg-shell.

larval instars. In the first the form is of a typically Buprestid, flattened "tadpole" outline; in later stages it becomes more cylindrical. In all three the wedge-shaped head is deeply sunk in the flattened and heavily chitinized prothorax. Toward the last larval instar a pair of prolegs of a rudimentary unarmed sort develops at the rear end of the ninth abdominal segment.

The larva mines first in one direction and then in the

other, rarely crossing the midrib of the leaf, making a blotch of very variable form, devouring all the tissue between the two layers of epidermis. It lives solitary, except that confluence of adjacent mines may sometimes occur. The cast skins left at the center of the mine among the dried frass indicate that the larva returns here to moult. Here also in this most spacious portion of the mine it transforms. The naked pupa, at first soft and white, soon becomes hard and brown.

The egg stage lasts about ten days, the larval stage three to four or more weeks; the pupal stage about ten days. The adult lives ten months or more, emerging in August, feeding on the uninjured portion of the bulrush leaves, already blotched with mines, until their margins are notched and jagged; and the females, at least, feed again in the late spring when new leaves are available. At Ithaca, New York, they deposit most of their eggs in June. The beetle is about a sixth of an inch long, black, shiny, given to death feigning when disturbed, with short legs and antennae that fold compactly into grooves, making the ventral surface almost as smooth as the back. This bulrush grows on low ground that is often inundated in winter. Where the adult beetles hibernate is still unknown.

FAMILY CHRYSOMELIDAE

Leaf beetles

Among the sixteen genera of this great family that are now known to contain leaf-mining species, there is considerable diversity of form and habit. The larvae of all are depressed but some are otherwise little modified in adaptation to mining. They have well developed legs and rather ordinary head capsule, but the larvae of Octotoma are legless, and strongly wedge-shaped at the front; and they have thin flat mouthparts that are capable of feeding upon the

cells of a single layer (usually the palisade layer). Full depth mines are, however, the rule in this family, with equal visibility from either side of the leaf, and blotch mines are much commoner than linear ones.

As in the Lepidoptera, the more specialized show a preference for the longer enduring leaves of woody plants. The leaf-mining flea-beetles of the genus Phyllotreta feed on cruciferous plants. Those of Hippuriphila feed on docks (Rumex).

Among the various tribes of this great family only three, have representatives that mine in leaves. Among the flea beetles leaf mining is the exception, but among the "little leaf-beetles" (so Harris calls them) it is the rule. The larvae of the former are but little specialized for mining, being almost cylindrical and possessing well developed thoracic legs. They are not found in very thin leaves but rather in the thicker more succulent ones, as those of some of the cresses. The larvae of the latter are somewhat depressed. They have short, widely separated thoracic legs. The abdominal segments protrude at the side as somewhat triangular tubercles. The mines which these make are somewhat inflated and bladder-like.

Hispinae. These little wedge-shaped leaf-beetles are more abundantly represented in the tropics than farther north. The larvae of several species are known to be leaf-miners. The adults have the antennae inserted close together. In most of the species, as the name Hispa suggests, the wing covers and prothorax are roughened by deep pits or are covered with long sharp spines. Many of the beetles are brilliantly colored.

Hispa

Of the genus Hispa, from which this tribe takes its name, we have not, so far as known, any North American repre-

sentative. Species of genus which mine as larvae are well known in Europe and Asia. In the case of *Hispa testacea*, Sharpe recounts that it mines the leaves of *Cistus salviaefolius* in South Europe. It has the habit of occupying two different leaves, one of which it enters soon after hatching. When it has hollowed about three-fourths of the first leaf it ruptures the epidermis of the upper surface and seeks another leaf. This found, it places itself on the midrib, tears the upper epidermis, and lodges itself in the leaf. In the case of the second leaf, the larva attacks the parenchyma in the neighborhood of the petiole and forms an irregular tube which has an open mouth at the point of entry. In this tube it completes its metamorphosis.

Chalepus and Baliosus

These two closely allied genera contain a number of leaf-mining species the best account of which is that of Chittenden (1904), from which we borrow both facts and figures.

These are very pretty little beetles, something less than a quarter of an inch long, sometimes colored brightly in orange or red and black, and having the wing covers elegantly sculptured with large pits arranged in double rows between raised longitudinal ridges. The commoner species are thus strongly marked, and easily recognizable.

The leaf-mining locust beetle, *C. dorsalis*, is perhaps the species best known, on account of the midsummer damage it does to the leaves of the black locust (*Robinia pseudoacacia*). "In cases of severe attack the leaves turn brown as if scorched by fire."

The adult beetles make their appearance in early spring as soon as the locust leaves are fully developed. They are small, less than 6 mm. long, and so strikingly colored as to be easily recognized. They are bright orange red above, with the head and a stripe along the suture of the wing cases black. The underside and legs are also black. Each wing

has ten series of punctures and three of the interstices form elevated ridges. These beetles are to be seen apparently motionless upon the leaves; but if they be closely examined they will be found feeding. While the leaves are young they eat out small oblong holes but later in the season they eat only part way through the parenchyma. The beetles are usually rather inactive and walk but slowly. If disturbed, however, they take flight and go for a long distance before settling again.

The eggs are laid on the underside of locust leaves in small masses of three to five, glued together, and partially

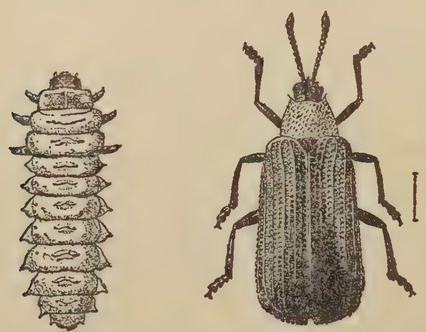


FIG. 62. The leaf-mining locust beetle *Chalepus dorsalis*. *a*, adult; *b*, larva; *c*, pupa. (From Chittenden.)

covered with excrement. The first egg of the mass is laid flat on its side and the others partly overlap the first one and, therefore, stand obliquely, with one end of each egg touching the leaf surface. A brown spot soon appears on the upper leaf surface, marking the location of the egg mass beneath.

The larvae on hatching enter the leaf under the protection of the egg mass, all through a single hole that is made by the larva that hatches first, and all of them occupy one common mine. They consume all the mesophyl within

the mine. In from two to four days, after having eaten half or more of the first leaf they leave the mine and wander to other leaves and separately make new mines, each on a leaf and in a mine of its own. There are several such changes of habitation, and the damage to the tree is greatly increased by this uneconomical habit. The larval life appears to last about 3 weeks.

The larva is rather unspecialized for a leaf-miner. It is only a little depressed and not much narrowed behind the prothorax. The second and third segments of the thorax are distinctly wider than the first. Legs are well developed. The body is yellowish-white, with darker chitinization of head, prothoracic disc, legs and dorsum of anal segment. The abdominal segments are triangularly produced at the sides each into the thin, flat, spine-tipped tooth.

Pupation occurs within the mine and the pupal stage lasts a week or ten days. The adult beetle, emerging breaks its way out through the thin and brittle epidermis of the leaf. There is apparently a single brood annually northward with more than one in the South. The adult beetles hibernate.

Several other species of Chalepini are known in North America. Those of which the life histories have been worked out are all leaf-miners. The best known, *Baliosus ruber*, attacks the leaves of several trees including white oak and apple, but its favorite food plant seems to be the linden. It, too, hibernates as an adult and begins depositing eggs in late May or early June. Another, *Baliosus californica,* was reared by Mr. Coquillett from larvae mining in the western *Ceanothus integerrimus. Anoplitis inaequalis,* has been bred from the white snake root, *Eupatorium urticifolium,* and from the wild sensitive plant, *Cassia nictitans.* Another, *Chalepus bicolor,* was reared by Mr. Pergande from the leaves of the panic grass, *Panicum macrocarpum.*

Octotoma

The trumpet-vine leaf-miner, *Octotoma plicatula,* is a related form that mines the leaves of *Tecoma radicans.* Its mines "consist of several sinuous branches starting from the midrib." The pupa is "always to be found in a pocket adjoining the midrib."

Microrhopala

Of the genus Microrhopala, we have several North American species. Such larvae of this genus as are known mine

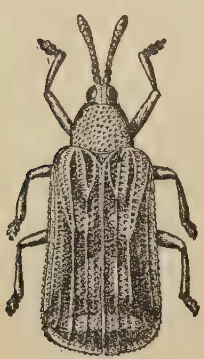


FIG. 63

FIG. 64

FIG. 63. The leaf-mining linden beetle *Baliosus ruber.* (From Chittenden.)

FIG. 64. The leaf-mining beetle of the Virginia Creeper, *Octotoma plicatula.* (From Chittenden.)

the leaves of various composites. The adults eat elliptical holes in the leaves. The larvae make long inflated mines. *Microrhopala vittata* has been found attacking various goldenrods.

The eggs are covered with a brown substance, evidently excremental. They have been found among the hairs on the lower surface of the leaves and are usually placed in groups of three or four near the tip. *Microrhopala xerene* has been reared from various goldenrods and asters and also

from plants of the genera Boltonia and Sericocarpus. The eggs are smaller than those of *M. vittata* and they are closely appressed to the surface of the leaf. They are covered with dark, nearly black excremental matter. They are usually deposited on the under surface of the leaf near its edge and remote from the petiole.

The larvae are able to migrate from leaf to leaf and to re-enter the parenchyma. The mines are blister-like, variable in size and shape and they often occupy a large share of the leaf. As many as four larvae may develop in a single large leaf. At the point in the mine where pupation occurs it "puffs up so as to form a hard blister, more or less rounded oval in shape, and usually a little over an eighth of an inch wide." Such cells have been observed at Washington, D. C., as early as tenth of June. In hot weather the pupal stage lasts from four to six days. The full grown larva measures from 6 to 6.5 mm. and the pupa about 5.5 mm. The pupae, like those of the locust leaf-mining beetle are capable of forward movement.

A Southern species, *Microrhopala floridana*, was reared by Messrs. Hubbard and Schwarz from larvae found mining terminal portions of the leaves of the grass-leaved golden aster, *Chrysopsis graminifolia*, in Florida.

Stenopodius and Uroplata

Single species of these genera are known to mine leaves; *Uroplata porcata* on Panicum capillare reported by Frost (1924) and *Stenopodius flavidus* on Sphaeralcea grossulariaefolia reported by Jones and Brisley (1925).

Halticinae. Most of the so-called jumping or flea-beetles feed on the surface of leaves or burrow in stalks or roots, but some of the smaller species insinuate themselves into leaves. The beetles are capable of leaping about by reason of their greatly thickened hind femora or thighs. As adults

they feed upon the leaves, perforating thinner ones and digging pits into thicker ones. In the winter they conceal themselves in dry places under stones, in tufts of grass and moss or in the chinks of walls. They lay their eggs in the spring upon the leaves of the plants which serve them for food. Harris in "Insects Injurious to Vegetation" says of their larval habits:

> The larvae or young of the smaller kinds burrow into the leaves and eat the soft pulpy substance under the skin, forming therein little winding passages in which they finally complete their transformations. Hence the plants suffer as much from the depredations of the larvae as from the beetles. The mining larvae are little slender grubs tapering toward each end and provided with six legs. They arrive at maturity, turn to pupae and then to beetles in a few weeks. Hence there is a constant succession of these insects in their various states throughout the summer.

None of the larvae are greatly specialized for mining. All are more or less cylindrical tapering at the extremities and supplied with well developed thoracic legs.

Dibolia

The plantain flea beetle, *D. borealis*, attacks the broad-leaved *Plantago major*, and fills its leaves in early summer with irregular linear mines, that run for the most part lengthwise of the leaf, and that are often lobed and branched and anastamosing. The miner is a minute yellow larva having a blackish head and a longitudinally divided prothoracic shield. It is but little depressed; and as the leaf is thin it lifts the epidermis and leaves it a little elevated like the roof of a mole-run in the soil. (See fig. 57, 3.)

The yellow eggs are laid on the upper surface of the leaves in the spring in small holes that are made by the female with her jaws for their reception. They are partially covered with blackish excrement. The larvae on hatching at once

enter the leaf. If the leaf becomes too dry or the space within it too crowded, the larva will leave its mine and crawl about in search of a place to start a new one. Cutting a slit in the epidermis, it may readily re-enter by eating its way in.

The larva when grown leaves the mine and descends an inch or less into soft soil to form a pupal chamber there. It emerges as an adult about two weeks later. In the northern United States there is a single annual brood, but in the latitude of Washington and southward two generations occur.

Phyllotreta

The flea beetles of this genus are widely known as pests of cruciferous plants. The adults of the various species feed upon the leaves of our various cultivated cruciferous plants, such as cabbage, radish, turnip as well as upon various wild cresses and weeds. In the larval state some of the species live in the interior of the leaves while others are subterranean in habit and feed on roots. *Phyllotreta vittata* according to Comstock, Chittenden, Thomas and others, has the latter habit. The grub is described as small and slender and almost entirely white. The pupa is said to be found in a little earthen cell a few inches deep in the soil. *Phyllotreta nemorum* of Europe and *Phyllotreta sinuata* of North America, on the other hand, mine in the interior of leaves in the way described by Harris. It is probable that others of our species do likewise. According to Miss Murtfeldt *Phyllotreta sinuata* breeds chiefly in the leaves of pepper grass (Lepidium spp.) and rock cresses (Arabis spp.). Chittenden (1923) lists *P. zimmermanni*, *P. liebeckei* and *P. aeneicollis* as leaf miners.

The cucumber flea-beetle, *Epitrix cucumeris*, is said by Comstock and others to be a further example of a flea-beetle with a mining larva. This is a common pest on cucumber and melon vines. It is also known to attack potato, rasp-

berry, turnip, cabbage and other plants. The beetle is a small black species, measuring less than a twelfth of an inch in length and possessing yellow antennae and legs.

Sagrinae. This small tribe is represented in our fauna by the following single leaf-mining genus.

Zeugophora

The cottonwood leaf-mining beetle, *Z. scutellaris*, makes great black blotch mines on the upperside of the leaves of poplars, often seriously disfiguring and damaging the trees. (See fig. 54, 2.) The following notes of this species are based on Strickland's excellent paper (1920), together with observations made by the senior author at North Fairhaven, New York, while obtaining the additional data on larval head structures already given in the introduction to this chapter (p. 185).

Before egg-laying begins the adult beetles feed openly upon the leaves nibbling at the first leaves of the season, eating out little patches of parenchyma generally from the underside, leaving the upper epidermis intact. A brownish corky tissue later develops around the injured area. Other smaller holes are also made for the reception of the eggs. The eggs are thrust singly into these latter holes, that extend from the lowerside puncture diagonally upward. After the egg is inserted, the injured tissue about it turns brown, and a spot of that color about 1 mm. in diameter appears upon the green upper surface.

The egg is short, cylindric or oblong, measuring about 1.5 mm. Judging by the cast skins found in the mines, there appear to be three larval instars.

The larva on hatching begins at once to cut a way through the palisade tissue next the upper epidermis. Only rarely is a mine found next the lower side of the leaf, and then only the lowermost layers of mesophyll are eaten. The tissue

left exposed and uneaten soon turns black and an old mine is all black except for the small marginal lobe in which a larva is still at work.

The larvae are essentially solitary, except when two or more mines on a single leaf become confluent and then they feed widely apart. Usually only a single living larva is found in even the large compound mines when completed, the several dead ones are often present.

When grown the larvae break through the loosened epidermis and fall to the ground and bury themselves there before transforming to pupae. They enter upon hibernation curled up in a little oval earthen cell hollowed out in the soil several inches beneath the surface.

The adults are black and yellow, oblong beetles, about an eighth of an inch long, with coarsely punctate elytra. There is a prominent tubercle on either side of the prothorax, the elytra and abdomen are black and the remainder of the body is yellow.

FAMILY CURCULIONIDAE

It has long been known that the larvae of a few of the snout beetles live in tunnels in the interior of leaves and then pupate in the mines either free or in silken cocoons. Frisch, 1721, Reamur in 1737 and Swammerdam in 1758 all give accounts of weevil miners. Reamur figures the larva of one. All these undoubtedly refer to members of the genus Orchestes, to which genus most of the weevil miners belong.

Of this, the largest family in the world, only a few members are leaf-miners and these few are not very different as larvae from their stem-boring allies, only a little more flattened, and less arcuate in form. The larvae are legless. The prothoracic dorsum is chitinized only at the front. The body is widest across the base of the abdomen and there are deep incisures between the abdominal segments

separated by thin flat expansions at the lateral margin. The adult beetles feed upon the leaves. When their eggs are mature the females bore oval holes through the epidermis with their beaks and then oviposit in the holes.

Perhaps the most interesting thing about the leaf-mining weevils is the cocoon which some of them make. Many beetles form a pupal cell of earth or wood by pushing about loose materials surrounding them, but few indeed spin cocoons of silk as these do. If we pick up one of these larvae which has begun to spin its cocoon we may notice that the thread of silk issues, not from the mouth as in caterpillars, but from the anal opening.

Traegardh has shown in the case of *Orchestes quercus* that the malpighian tubules are very large. These appear to be the source of the fluid silk. The conical and rather sharply pointed final body segment is used as an implement for distributing and fastening threads of silk. The completed cocoons are nearly spherical in form and are of a firm strong texture, well fitted for protecting the delicate pupae within them.

In North America, leaf-mining weevils apparently occur in but two genera, Orchestes and Prionomerus. There is in Europe, a species *Cionus olens*, which mines the young leaves of various mulberries, making a puffed mine in which it afterward spins a rounded cocoon. Then Bargagli mentions *Rhamphus aeneus* and *Brachonyx pineti* as miners. The latter lives in the needle-like leaves of the Scotch fir, *Pinus sylvestris*. There are, too, a few species of Apion which mine in the midribs of fleshy leaves, as of thistles, sunflowers, sorrels and others.

Prionomerus

Of this genus only a single species occurs in northeastern North America. It is the sassafras mining weevil, *P. calceatus*, and it ranges with its host plants, the sassafras and tulip

tree, from New England to Michigan and south to Florida. It is a small, broad, black beetle three to four millimeters long, with a stout beak about as long as the thorax and with the front legs strongly incurved. In each of the front thighs is a wide tooth with a serrated front margin.

The females insert their eggs in a series along the midribs of the leaves in the spring. The larvae, entering the tissue, make large communal mines which inflate when dry. In preparing for pupation each larva spins a rounded cocoon of silk. These will be found clustered at one side of the mine. Beetles have been taken only in the spring and there is apparently but one generation a year.

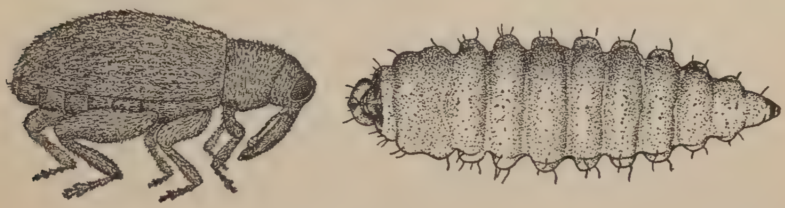


FIG. 65. Adult and larva of the leaf-mining weevil *Orchestes pallicornis*. (After Houser.)

Orchestes

Of this large genus nine species have been taken in northeastern North America. Those whose transformations are known are leaf-miners, chiefly on oaks, alders and willows. As most of the species are rare or infrequent it is not surprising that the biology of the group is incompletely known. Of the nine only one has been discussed at any length in literature. This species, the apple weevil miner or apple flea-weevil, *O. pallicornis*, has been injurious to apple trees in Illinois and has been studied by Forbes, Flint, and others. It is a small black snout-beetle about an eighth of an inch long. Its eyes are very large and almost meet in front. The beak is only slightly curved and rather stout. The hind femora or thighs are thickened and enable the beetles to leap about

very actively. If disturbed they will sometimes drop to the ground and feign death. This is one of the least uncommon and most widely distributed of our weevil miners. It ranges from Nova Scotia to Quebec through New England to Oregon and south to Texas. It has been taken on willows and shad bush and found mining the leaves of elm, alder, cherry and apple.

This weevil is single-brooded. The adults spend the winter among leaves and grass, under clods, or in cracks in the soil. When the frost has left the ground in the spring they become active and ascend to the branches of the trees. As the leaves appear they feed on them and soon begin depositing their eggs. The female gnaws out a longitudinal cavity in the under side of one of the major leaf veins. Moving the ovipositor over this hole she deposits in it a smooth, yellowish, bluntly rounded egg. This process is repeated at intervals for about a month. The wound made by the female in depositing the egg produces a slight swelling and a subsequent bend in the vein.

The eggs hatch in four or five days. In feeding the larvae at first make linear mines winding towards the edge and usually towards the tip of the leaves. There, changing their method of feeding, they gnaw out a blotched portion which becomes somewhat inflated. The mines become brick-red in color and are then quite conspicuous.

The larvae are somewhat depressed, yellow in color, and when fully grown are about three-sixteenths of an inch in length. They are broader near the head and after the sixth segment generally decrease in width. The last segment is very narrow and ends in a rather acute point.

The larvae feed in the leaves for about three weeks. They then construct rounded cocoons in the inflated portion of their mines. After a brief period as soft white pupae they transform to beetles and gnaw their way out. (See fig. 57, 5.)

The first beetles of a new generation begin to appear

about the time the beetles of the over-wintering generation die, i.e., about the middle of May in southern Illinois. For the ensuing four or six weeks the beetles of the new generation feed on the foliage of apple and other trees and fly from tree to tree. Before midsummer they descend to the ground, creep away into trash, grass or soil and there remain for the remainder of the summer and following winter apparently without food.

Orchestes rufipes is known from Quebec and Newfoundland to New York and west to California. It was found by H. H. Knight mining the leaves of the shining willow, *Salix lucida*, at Batavia, New York. The beetles were feeding on the leaves for the first two weeks in July and the grubs were found in the leaves during August and September.

Of European species one is a miner in oaks, one in birch, one or more in willows and poplars, and over 50 other species probably many of them leaf miners.

CHAPTER XIII

Order Hymenoptera

The few leaf-miners of this order all belong to the single family of sawflies, Tenthredinidae. It is a large family of rather primitive forms for the most part given over to general leaf-feeding.

In manner of life there is an interesting parallelism between these lowly Hymenopterous miners, and the primitive Lepidopterous ones of the family Eriocraniidae. In both groups apparatus is developed for inserting eggs in the leaf tissue. The eggs of the two groups are similarly large and membrane-covered and swell after insertion to twice or more the original size. Even the mines of the two groups are strikingly alike—blotched, transparent, with some of the fibrovascular system removed and with a large amount of excrement. Representatives of both groups are to be found mining in the early spring before most other miners appear. In the rapid feeding up, in leaving the mine, in entering the ground, in spinning the cocoon, there is a great similarity. In both, the feeding period is short—hardly more than two weeks; in both, the pupal period is short—something less than a month; in both, the adults live but a few days; and in both, a very large part of the year is spent as inactive larvae in a silken cocoon in the ground. Ecologically the two groups are remarkably exact counterparts.

The eggs. Many of the leaf-mining sawflies, in common with the remainder of their family, have the habit of inserting their eggs in the interior of leaves. A cut is made for each egg separately through the leaf epidermis not infrequently in the axil of a lateral vein. The egg-slits are made by the ovipositor of the female operating in much the fashion

of a saw. This ovipositor is composed of two finely serrated chitinous blades, which lie side by side, and may be projected from a protective sheath and moved with a saw-like motion. The egg is slipped in before the saws are withdrawn. After being laid, through the taking up of moisture or for some other cause, the eggs swell to twice or more

THE LEAF-MINING GENERA OF HYMENOPTERA*

FAMILY SUBFAMILY	GENUS	DISTRIBUTION	NUMBER OF DESCRIBED SPECIES	NUMBER OF MINING SPECIES
Blasticotomidae	Blasticotoma	Eur.	1	1†
Tenthredinidae				
Phyllotominae	Phyllotoma	Eur.	6	6
	Phlebatrophia	Eur., N. A.	2	2
Holocampinae	Heptamelus	Eur.	1	1†
Dineurinae	Pelmatopus	Eur.	6	4
Scolioneurinae	Entodecta	Eur., N. A.	6	2
	Scolioneura	Eur., N. A., S. A.	7	6
	Metallus	N. A.	5	4
	Parabates	N. A.	2	0
	Polybates	N. A.	1	0
Fenusinae	Profenusa	N. A.	1	1
	Fenusa	Eur., N. A.?	3	3
	Kaliofenusa	Eur., N. A.	2	2
	Messa	Eur., N. A.	1	1
	Fenusella	Eur.	11	3
	Fenella	Eur.	4	2
Schizocerinae	Schizocerus	Eur., N. A., S. A.	22	2 or 3

* From Frost, 1925.
† Petiole miners.

their original size, causing the leaf to bulge up in little mounds.

Embryonic life lasts from twelve days to two weeks and at the end of that time the little larvae may be seen fully formed and coiled up within the membrane of the eggs.

With transmitted light and a good lens one may watch the process of emergence from the egg into the leaf tissue. Most sawflies emerge almost at once and feed on the surface of the leaf but the true miners tunnel slowly upwards towards the upper epidermis. Then, hanging upside down from the upper cuticle, they tunnel through the parenchyma and the finer divisions of the fibrovascular system. In feeding they take rapid nibbling bites directly in line with the long plane of their bodies. They turn the head and body from side to side but in no case bend their heads alone to feed on the exposed surface. They hold to the walls of the mine chiefly by the posterior parts of the body. In *Metallus rubi* the anal legs are somewhat fused and ridged at the base with chitin. This gives them an anal sucker effectively employed in holding and in moving about.

Most of the leaf content is consumed. On the upper side remains the cuticle with a faint tracery of the fibrovascular pattern adhering to it. This tracery of filbrils distinguishes at once a sawfly mine from the blotch mines of the sap-feeding Lepidoptera, in which the cuticle is left entirely free of any other tissue. On the lower side there is besides the cuticle, usually a greater share of fibrovascular tissue than is on the upper side—especially in leaves in which the veins are prominent below; and, in the thicker leaved host plants, as alder, some residual parenchyma. Most sawfly mines are very transparent. Scattered through the mines is an abundance of excrement in very black cylindrical fragments perhaps four times as long as broad. The larvae seem bigger in proportion to the mine than most lepidopterous miners. They are not greatly depressed and they cause the mines to become somewhat bulged. Large veins partly determine the limits of the mines.

The larva. In form, the larvae are generalized rather than specialized miners. They are considerably depressed and somewhat moniliform; the somewhat triangular head-cap-

sule is in alignment with the long axis of the body until the sixth stage; but they are tissue feeders from the beginning. In many the thorax is wider and thicker than the abdomen, especially so when young.

The depressed, somewhat triangular head-capsules are nearly twice as broad as long. The mouthparts project in front. There is never more than a single ocellus on either side of the head. This will distinguish them from most lepidopterous miners. In these, as in lepidopterous miners there is a tendency for the front to extend farther towards the vertex than in free-feeders. In Scolioneura the stem of the epicranial suture is only about one-half the length of the arms and the caudal end of the front is an acute angle. In sawfly larvae there are no sclerites corresponding to the adfrontal plate of caterpillars.

Thoracic legs are present and are from one to five jointed. Their position is far to the side and between them in line with the abdominal prolegs secondary protuberances are sometimes developed. In most miners the thoracic legs are not much used, but *Metallus rubi* continues to make some use of them. Abdominal prolegs are present on segments 2, 3, 4, 5, 6, 7 and 8 of the abdomen. *Profenusa collaris* is represented to have slight protuberances on the 1st and 9th segments also. Anal prolegs are present in some miners, lacking in others. When present they may be separate, or fused to a conical stump and perhaps ringed around at the base with chitin. In no sawflies are hooks (crotchets) developed on the prolegs and in the miners, especially in the early instars, prolegs are much less prominent than in the free-feeders.

In color the mining sawflies are greenish white or pale green, the color being largely due to ingested parenchyma. The head capsule is usually brownish; honey-brown or darker. The prothoracic shield is always present and may be dark in color. Sometimes the second thoracic segment

has some dorsal markings also. On the ventral side spots are common at least on the thoracic segments. In mining, the venter is uppermost, sheltered only by the leaf's thin cuticle, and these spots perhaps protect the nervous ganglia.

These sawflies moult six times as larvae, five times in the leaf and a sixth upon going into the pupal state. The five moult skins are usually to be found in the mine. Instead of finding the head capsule in one place and the body covering in another, as in lepidopterous miner moults, these are wont to be in one piece, with a slit through the vertex of the head capsule and through the prothoracic shield. In moulting the head and thorax are first worked out through the slit and then by a series of wriggling movements the shell is worked down the body and off the anal segment. The thin body cuticula beyond the prothoracic shield may be turned partly inside out in the process or is at least very much drawn and wrinkled.

Except in size and the increasing visibility of appendages the larvae change but little from instar to instar until the sixth. The head capsule becomes slightly more oblique by the fourth and fifth instars. In the sixth instars the head capsule becomes vertical. The larvae are now less depressed and moniliform and are usually without spots of any kind. In this stage they do not feed but members of the Fenusinae and Scolioneurinae break through the upper cuticle of the mine, crawl to the edge of the leaf fall to the ground, enter the earth to a depth of not more than a few inches, and there make a slight cocoon of silk and particles of earth. If some of the cocoons be sifted out of the earth in the months after the larvae have entered the ground (and these are hard to discover even in breeding boxes where the quantity of earth is small and the larvae are known to be present) they will be found to contain white inert larvae with the head bent forward and the thorax somewhat humped. In this state they continue for the greater part of a year. Compound

eyes and ocelli form months before the pupal stage is attained and the adult characters of the head may be plainly seen through the skin of the larvae shortly before the last larval moult.

To enter the ground (or, in some cases, rotten wood) in preparation for pupation is a very common habit among sawflies, but the leaf-miners of the Phyllotominae have departed from the habits of their relatives and developed, for sawflies, very eccentric methods. Three or more species of Phyllotoma in Europe are reported to spin in the sixth instar circular disclike cocoons in the leaf. One of them, *Phyllotoma aceris*, goes so far as to spin this cocoon in the leaf and to free it by cutting out the circular piece of the leaf's upper cuticle to which it is attached. Case and larvae blow to the ground where pupation takes place late the next season.

The pupae. The pupae are pale, whitish, greenish or yellowish in color. The antenna, leg and wing cases are free, and the wings are pad-like. In twelve to fifteen days after the pupae are revealed the adults emerge from the pupal skin. When the wings are fully expanded and the chitinous parts hardened they roughly cut away one end of the cocoon and work up through the soil.

The adults. Adult sawflies of the particular species adapted to leaf-mining, though some are giants among miners, are never-the-less small compared with the adults of free-living sawfly larvae. After emergence they may be found about their host plants mating and ovipositing, or on cold, dark days hidden away in a cluster of leaves or a crevice of bark. Some have but one generation; the majority have two.

PHYLLOTOMINAE

Most of the known Phyllotominae are European in distribution. According to Professor A. D. MacGillivray, most

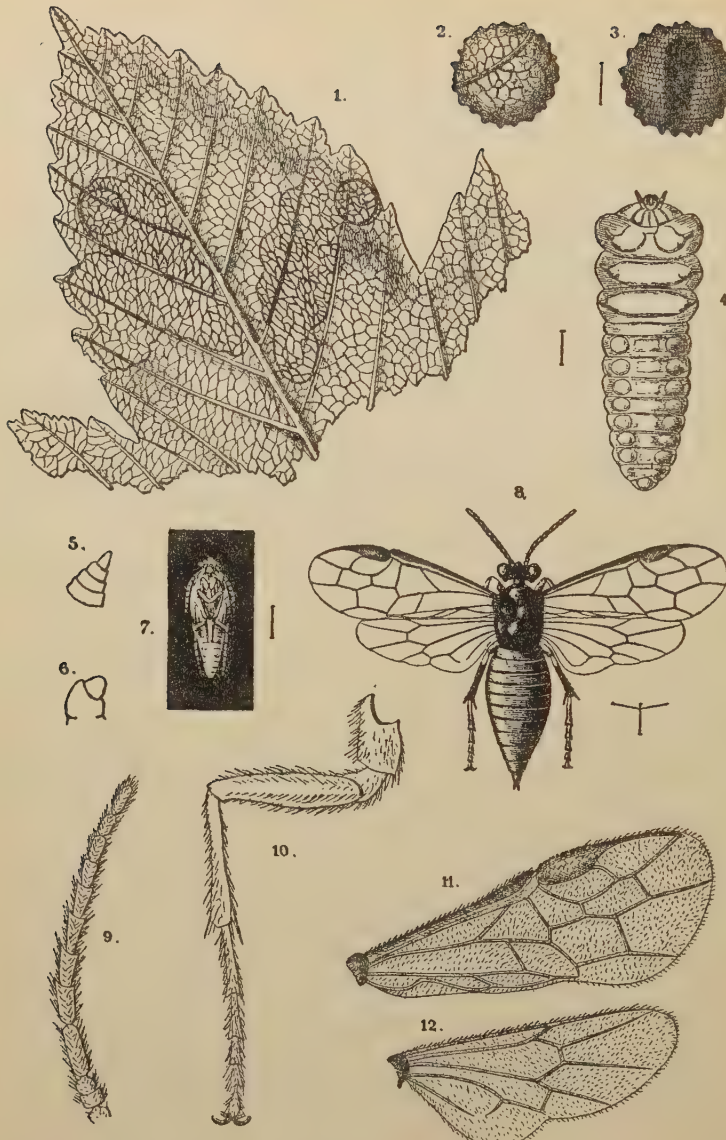


FIG. 66. The maple saw-fly leaf-miner, *Phyllotoma aceris*. *1*, maple leaf, showing mines and cocoons; *2*, epidermal cap covering cocoon; *3*, cocoon with pupa; *4*, larva, ventral view; *5*, antenna of larva; *6*, spinneret of larva; *7*, pupa; *8*, adult; *9*, antenna of adult; *10*, front leg of adult; *11*, *12*, wings of adult. (After Ritzema Bos.)

of the members of this subfamily feed from the under surface of the leaves eating away the lower parenchyma. There are, however, in the type genus Phyllotoma and in Phlebatrophia, several examples of miners. The European *Phlebatrophia nemorata* has recently been reported as mining leaves of birch in Nova Scotia. It has probably been recently imported. One of us (Mrs. Tothill) has observed this leaf-miner in Nova Scotia and has found that it has the habit of spinning a silken lens-shaped cocoon within the mine.

Stranger still is the habit of *Phyllotoma aceris* mentioned above. The following account of this insect together with figures we take mostly from an excellent article by Professor Ritzema Bos (1900). The adults of the phyllotomid miner of maple, *Phyllotoma aceris*, emerge about the first of May in Europe at which time the trees are usually well in leaf. They soon pair and the females begin to lay eggs in the leaves of maples, especially *Acer campestre* and *Acer pseudo-platanus*. The eggs are usually placed near a lateral vein. They soon hatch and the larvae grow rapidly, becoming full-fed before the end of June. In feeding the upper and lower cuticles and, at least in large part, the veins are left undisturbed. The mines, though often extending beyond two or three of the main lateral veins, never cross the midrib. At first the mines show as white spots but later become more darkened as dampness scatters the color of the excrement. There may be from one to five mines in a leaf but with only one larva in a mine. The number of moults has not been certainly determined but the skins are shed in one piece. The frass is loose and dry in the mine and therefore shakes about.

The full-grown larvae are 6 to 7 mm. in length, somewhat broad and short and more or less oval in cross-section. There are three broad thoracic segments and ten successively narrower abdominal ones. In color they are white

to bluish-gray and sometimes tinged with yellow. The thoracic legs are four-jointed with a broad basal and a narrower second segment. The seven pairs of prolegs are short, blunt and little used. At least on the younger larvae are brown to black, chitinous spots on the dorsal side of the prothorax and on the ventral side of all the thoracic segments. In the later instars the larvae are rather stout and dilate the upper sides of the mines.

When about full-grown they eat out the parenchyma from a part of the leaf at one border of the mine making an outpushing a little more than 6 mm. in diameter. There they spin lens-shaped cocoons which on one side are applied to the upper cuticle of the leaf. This cuticle is gradually cut through at the border of the cocoons and presently the cases with their covering of leaf epidermis on one side and their thin sheet of weaving on the other are freed from the leaves and fall to the ground. All the frass and cast skins are left outside the cases which are semi-transparent, revealing the larvae within. Somewhat flattened though the larvae be they cause the walls of the cocoons to bulge. On the ground the cases look not unlike little seeds. The deserted leaves present a peculiar appearance with mines of which the lower walls are intact, while the upper walls have every one a neat round piece removed.

In these cases on the ground the larvae remain until the following season in late March or early April when they assume the pupal state. In the months after leaving the leaves they are said to be able to cause their cocoons to hop on the ground by their powerful movements within. Professor Ritzema Bos says that they sometimes jumped 5 to 10 mm. off the ground and C. Healy makes the statement that they move on the ground by little hops. They are also moved passively by the wind. That they are sometimes very abundant locally is suggested by the somewhat remarkable statement of Mr. McLachlan (Proceedings

of the Entomological Society of London, 1877, p. xvii) that in an infestation of maples near Brussels "the flattened case formed by the larvae when full-fed made quite a pattering noise as they fell from the trees."

FENUSINAE

All the species of the Fenusinae, whose habits are known, have leaf-mining larvae. In America as well as in Europe there are several examples. Two or more of our species in this group have been introduced from Europe but some are probably native. Their eggs are inserted in the leaf. They mine in blotches. In the sixth instar they leave the leaves and enter the ground where at least most of the species make a slight cocoon of silk or salivary secretion and earth.

The elm-leaf sawfly, *Kaliofenusa ulmi* has been imported from Europe and in America it particularly attacks its chief European host plants, the English and Scotch elms. From these it sometimes spreads to the American elm. Its infestations of these European shade trees is often very severe. It was exceedingly common in Albany, New York, and vicinity from at least 1895–1900. For several years there was a very severe infestation on English and Scotch elms at Ithaca, New York. As high as 90 per cent of the leaves were sometimes infested; and as there were often five or even more mines in a leaf, and as almost every vestige of parenchyma was eaten out of the mined areas, the growth of the trees was very seriously affected.

At Ithaca the adults emerge early in May. In 1915 they were abundant on the trees by May 12th but some were still crawling up through the earth and a few were found just emerging from some cocoons obtained by sifting soil from below the trees. In cold or windy weather they will be found hidden away in the partly unfolded leaves at the tips of the branches but on warm sunshiny days they are active, flying about the trees and ovipositing. The eggs

are laid soon after emergence and the adults are short lived. The eggs are laid in the axils of the lateral veins of the leaf, the slits being cut apparently from the under side. At first the eggs are hard to locate but they soon swell to a diameter of about 0.5 mm. and are then very apparent just within the lower epidermis. In about a week after they become thus swollen the larvae may be seen curled within the delicate egg membrane. Feeding and wriggling they make their way into the tissue and up toward the upper epidermis of the leaf where they feed with the venter uppermost. They feed rapidly, extending the mine first between the two veins proximal to the place of hatching, but later increasing the area for half an inch or more along the mid-rib and involving most of the space from the mid-rib to the lateral border.

In the first 5 instars the larvae are white with a pale brown head. Beneath the 1st thoracic segment there is a black oblong plate sometimes with a dot on either side and on each of the succeeding segments except perhaps the last there is a small black spot appropriately placed for shading the nervous ganglia of the segments in the strong light upon the upturned venter. The six thoracic legs are lateral in position and not much used in progression. The prolegs on abdominal segments 2, 3, 4, 5, 6, 7, 8 and 10 are poorly developed.

In the sixth instar the larvae are 7 mm. or more in length. The head capsule is for the first time vertical to the plane of the body. There are no spots on the white body in this instar. The larvae now cease to mine but cut through the upper epidermis, crawl to the edge of the leaf and fall to the ground. The first larvae leave the leaf during the first week of June and by the middle of June most of the mines are empty. The larvae enter the soil to a depth of from one to three inches and spin small cylindrical brown papery cocoons. They remain the rest of the summer and the

following winter in these cocoons as untransformed larvae and the following spring in late April or early May transform through tender whitish pupae into adults.

This serious menace of these particular shade tree pests is not easily controlled by spraying as the larvae being within the leaf escape from much contact with the materials used. Nicotine sulphate has been used with some degree of success.

The alder sawfly (*Fenusa dohrnii*), is another imported pest attacking the European alder. It is reported to have been at Ithaca, New York as early as 1891 and was common there for several years previous to 1905. They mine the

FIG. 67. The cherry or hawthorn leaf-miner, *Profenusa collaris*. *1*, male; *2*, female. (After Parrott and Fulton.)

leaves of alders, especially the European ones, early in June. The blisters are large and often the mines so merge as to bring several larvae into a common mine. The example is from a European account by a Swedish writer, Ivar Traegardh. The life history is very similar to that of its near relative the elm-leaf sawfly.

The Cherry and Hawthorn Sawfly, *Profenusa collaris*, is a new orchard pest in New York. It is not recorded as injurious to fruit plantings until 1915. As a hawthorn pest this species is definitely known to occur in New York and Massachusetts and it is doubtless a native species. Almost the only notice of this species in our literature is a careful

and interesting account by P. J. Parrott and B. B. Fulton (1900), from which the following is abstracted:

The adult insect is a small sawfly which varies from 3 to 4 mm. in length. The body of the female is metallic black with the prothorax rufous in color. The sawflies make their appearance during early May at the time when the first leaf clusters are unfolding and the blossom buds are beginning to open. The eggs are laid singly through incisions in the upper epidermis. The lower surface of the egg usually lies in contact with the lower epidermis which has been cut free from the other tissues so as to form a small blister-like cavity or pocket. The egg is elliptical in shape and when released from the pressure of the leaf and increased to its greatest size, it is 5 to 7 mm. long and 0.28 to 0.36 mm. in diameter. The chorion is a thin, white, shining, flexible membrane. The majority of the eggs are deposited in the basal portion of the leaves.

Hatching occurs during the middle or latter portion of May. The young larvae work their way to the parenchyma immediately beneath the epidermis of the upper surface of the leaf and mine toward the distal end of the leaf generally keeping close to the lateral margin. The injury is first indicated by a sinuous channel which finally swells out into a large blister-like area. They are most conspicuous on the upper surface of the leaves during early June. The larvae are then making their maximum growth.

By collecting and measuring moulted skins it was ascertained that the larvae normally moult five times in the mine. The first instars are very much alike, differing in the first five chiefly in size. The body is widest at the first and second thoracic segment and gradually tapers toward the anal segment. The thoracic legs are short and conical and of five segments, which include a thick, basal and a small hooked terminal structure. All the abdominal segments except the last bear short, rounded prolegs on the ventral

side. The head is horizontal in the early stages but slopes downward slightly in the later instars and becomes vertical in the sixth. It is broad and flat, rounded on the sides, and obtuse in front.

The body is slightly less moniliform and depressed in the sixth instar. In this instar the larvae leave the leaves, enter the earth to a depth of several inches in the soil and construct an earthen cell. This cocoon is oval in shape and

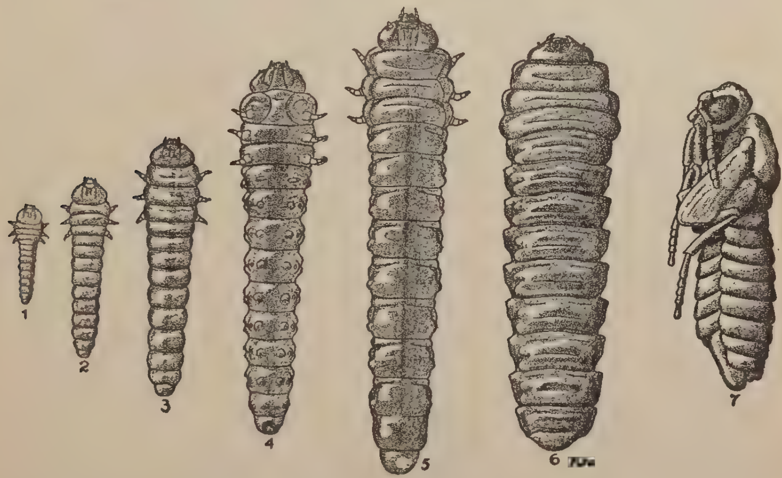


FIG. 68. The cherry or hawthorn leaf miner. *1–6*, larval instars; 7, pupa. (After Parrot and Fulton.)

consists of particles of earth glued together and lined with a sort of cement impervious to water. The larvae abandon the foliage and build this cell about the middle of June but pupation does not occur until late April or early May the following year.

Until the coloring of the adult begins to show the pupa is white in all portions except the eyes which are reddish. It is about 5 mm. long. The pupation period is very short, occupying hardly more than a week at the very end of April or beginning of May.

In outbreaks spraying with nicotine seems to be somewhat

successful in the case of hawthorn but to have very little influence in the case of cherry. This difference is doubtless due to differences in the cuticle of the leaves. Hydrocyanic acid fumigation was effective but is not practicable for ordinary cherry plantings. The one remedy recommended is that of picking the infected foliage early in the season.

Fenusa varipes. In the type genus of this subfamily there are an imported European and probably a native species. *Fenusa varipes* mines the leaves of native alders particularly *Alnus incana* in August and September. Dyar reports this species for the eastern states and Webster for Ottawa Canada and vicinity. In the fall of 1916 it was very common in the alders at Fredericton, New Brunswick. In late September and early October many larvae were still in the leaves. The larvae were found in the newer leaves at the ends of the twigs and on new shoots. These mines were nearly completed and the larvae left the leaves in a few days. There were also very many empty mines some of which seemed to have been recently vacated and others of which seemed to have been made much earlier in the season and so long deserted that the cuticles were dried and cracked and worn away. If all these mines were of one species then the species must be either double brooded or different individuals must vary greatly in the time of mining and emerging.

Mined leaves were brought into the laboratory and placed in tin boxes with damp earth. By the middle of October all the mines were empty and the larvae were buried in the soil. The completed mines were about 6 mm. wide and 30 mm. long, being confined for the most part between successive lateral veins. They were less transparent than other sawfly mines on such host plants as elm, rubus sp., violet or hawthorn. Both sides of the mines become dark brown and rather dry. The frass is abundant and scattered through the mine.

In the fifth stage the very flat head is honey brown with a a paler vertex. The mouthparts are dark brown. The prothoracic shield is pale brown with darker margins. The other segments are unmarked on the dorsum. On the venter the first three body segments are marked with pale brown. On the first segment the colored area covers most of the ventral surface between the first pair of appendages. The lateral margins of the colored area have a somewhat jagged and irregular outline. The color is deeper in a rounded spot at the center of the posterior margin. The spots on the two following segments are small and nearly round at the center of the segments. The thoracic legs are small, short, conical and very little used. Prolegs are slightly developed on abdominal segments 2 to 8 inclusive. There are no anal prolegs and there is no anal plate.

In the sixth stage the larva acquires a vertical head capsule and becomes rather more rotund in its proportions. The full-fed larvae are from 7.5 to 8 mm. long. After the fifth moult they feed no more but leave the leaves and enter the ground.

The yellowish pupae is to be found in an elliptical cell in the ground.

Fenusa curta. According to Dyar there is in the eastern States, a sawfly miner of Oak, *Fenusa curta.* He found the mines of this species on the upper side of the leaves of the bur oaks, *Qercus macrocarpa.* The completed mines were 5 to 10 by 30 to 15 mm. in extent.

His description of the fifth stage larva shows it to be like *Fenusa varipes* in many respects but he states that the thirteenth segment is divided by an incisure, the thoracic feet are black, the prothoracic shield is brownish black, and that there are spots on the venter between the thoracic feet. These ventral spots are probably darker than those of *Fenusa varipes* which he fails to mention. In the fifth and sixth instars a sub-ventral ridge is apparent.

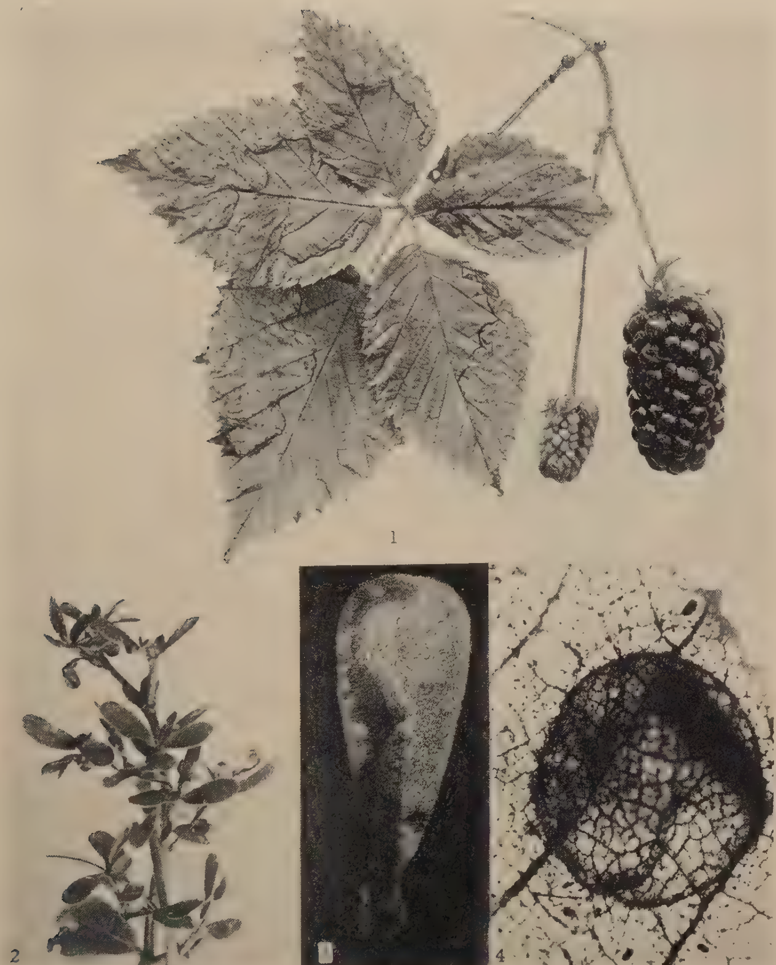
Its habits in leaving the leaf and entering the ground are entirely similar to those of the other Fenusinae.

SCOLIONEURINAE

Of the ten North American species of the subfamily *Scolioneurinae* enumerated by MacGillivray one is in the genus Scolioneura, four are in the genus Metallus, three in the genus Parabates and two in the genus Entodecta. So far as known these species are all leaf miners. More notice has been given in literature to miners of the genus Metallus than to members of others of these genera. Careful life-history observations on some of the other species are much to be desired.

THE BLACK-BERRY LEAF MINER

Metallus rubi. In the literature of economic entomology there have been four or five accounts of sawfly miners inflicting serious injury upon plantations of blackberries, dewberries or raspberries; and despite some discrepencies between these accounts they are now generally considered to refer to the single species, *Metallus rubi.* Discrepencies in regard to the time of mining are to be interpreted in the light of climatic differences. In Delaware according to Professor Houghton, the first brood emerging in spring begins ovipositing in late May. The larvae hatching from these eggs were full-fed by the end of June and transformed through pupae into sawflies early in July. The larvae of this second brood are full-fed by late July or early August. In New York and Illinois observations by C. R. Crosby and S. A. Forbes respectively indicate that the second brood of larvae are not full-fed until much later. Professor Crosby observed unhatched eggs of this brood on August 25th and Professor Forbes reports that the larvae had left the leaves and entered the ground by September 25th. At Frederic-



Hymenopterous Leaf-Miners

(Photographs by Dr. R. Matheson)

Fig. 1. A leaf of dewberry bearing mines of the sawfly, *Metallus capitalis*.

Fig. 2. A spray of purselane bearing mines of *Schizocerus Zabriskei*.

Fig. 3. One leaf from the same, more enlarged.

Fig. 4. Portion of a birch leaf bearing within a mine a hibernating cocoon of the sawfly, *Schizocerus mathesoni?*

ton, New Brunswick, the larvae are still in the leaves in early October. That the beginning and end of the generations is not sharply marked is apparent from the fact that larvae of different sizes are present in the leaves at the same time.

FIG. 69. Mines of *Metallus rubi* on blackberry. (Drawn by John D. Tothill.)

The eggs according to C. R. Crosby are usually placed near a prominent vein. They are to be found in blisters about 0.75 mm. in diameter. The eggs are nearly white, smooth, and somewhat flattened between the cuticles. The cavity previously occupied by these eggs can often be distinguished at the border of the mine.

The outstanding difference between this miner and Fenusid miners is in the character of the anal segment. The chitinous arcs almost surrounding the base of the anal prolegs allow the use of this area as a sucker in progression and in getting a purchase for mining operations. Holding with this it is also able to bend the forepart of the body from side to side more easily, a process which is aided and abetted by a greater use of the thoracic legs than Fenusid miners seem to exercise. When the cuticle above the larva is lightly touched with a needle it may be seen to take firm hold with the anal sucker and shake the body up and down vigorously —possibly a defensive action against parasites. If probed a second time it may shake itself again or may twist and turn itself away to another part of the mine.

In the sixth instar the larvae leave the mine by cutting through the upper cuticle. They enter the ground and there spin a thin cocoon of silk. The half-finished cocoon of a larvae sifted from the earth in a breeding box was found to be pale brown, composed of silken stuff spun into a parchment-like sheet, with a somewhat rough outside and a very smooth inside surface.

The miner are of the blotch type with the pellets of excrement more or less grouped and localized in the mines. The completed mines are about 30 mm. long by 10 mm. wide, or of similar area in different proportions of length and breadth. The position of the mines seems to be somewhat influenced by the size and position of the main veins.

SCHIZOCERINAE[1]

Our knowledge of the habits of the subfamily is still quite incomplete. The genus Schizocerus contains both leaf-mining and free-feeding forms. Yuasa (1922) speaks as though all of the species of Schizocerus may be leaf-miners

[1] Modified from Frost, 1925.

but several species as *ebenus* and *privatus* and the European *glomerata* are known as pests feeding externally upon the leaves of potato and rose.

According to Konow (1905) there are twenty-one described species of Schizocerus which are distributed as follows: four European, ten North American and eight South American species. With the addition of one species, *S. zabriskei* (see pl. 3) not listed by Konow, we can increase the number to twenty-two.

For our knowledge of the habits of the leaf-mining species of Schizocerus, we must rely chiefly upon Dyar, who has published several short papers upon this group.

According to Dyar (1897) *S. prunivorus* lays its eggs in a pyriform slit under the lower epidermis at the middle of one edge of the leaf. The larva hatches and eats a curious winding slit down into the leaf, later this reaches the edge. The larva drops to the ground, where it makes a cocoon of yellowish silk. Five instars are described.

Dyar (1893) describes the habits of *S. tristis fumipennis* a feeder of *Hosackia quadriflora* but does not state whether it mines. The cocoon is found on the back of the leaf. It is oblong rounded and composed of coarse silk of irregular texture and not compact enough to be opaque.

In 1900 Dyar described briefly the life history of *S. zabriskei.* The species is of special interest because it is one of the few Hymenoptera which leave one leaf, when the food is exhausted and start a fresh mine in another. Webster (1900) has described the species is more detail from whom we quote:

The eggs are deposited in the edge of the leaves, deposition usually being completed in ten to fifteen seconds. As soon as hatched the larvae begin to feed on the leaf, and ultimately mine out the greater part of the pulpy substance, but never eat through the surface until driven to do so from lack of food, whence they emerge and make their way to a fresh leaf, immediately enter

and continue their mining habit, apparently not feeding on the surface at all, except as they cut their way into the leaf. In numerous cases, where the obtainable leaves had all been exhausted, the larvae bored downward in the stem of the plant.

When fully developed, the larvae enter the ground to the depth of one-half to one inch and form a silken cocoon, to which bits of soil adhere quite firmly, and there transform. The pupa stage lasts only about seven days, when the adults emerge, a few males in advance, soon after which the sexes pair and oviposit.

The number of broods varies according to seasonal conditions but probably five is normal.

CHAPTER XIV

Order Diptera

The species of leaf-mining Diptera are comparatively few in number. There are scarcely sixty known leaf-mining species in America, and, while the inclusion of European forms would increase the list, even with these the total of known species is relatively small. Certain species are very prolific and abundant. Some have a large number of host plants, and can be found almost anywhere; while others are rarer, and are limited to a few hosts or even to one. A few species are so abundant that every leaf of their host plant may become covered with mines.

Most of the species have a general distribution throughout the country, but there are some which are found only in a limited area. The species may be divided generally into eastern and western groups. Certain species are further limited by the localization of the plants on which they occur. Still other species appear to be restricted to certain patches of plants, although the same species of plants are abundant in other places in the near vicinity.

Many of the species are European forms which have been introduced into the United States and have not spread far from their point of introduction. Boston, New York, and Washington are the chief points in the East where species have been introduced, and these are centers of infestation.

The eggs. In the Anthomyiidae, the large and conspicuous eggs are laid on the lower side of the leaf. The ovipositor, as might be expected, is very simple; there is no need for specialization in such a method of egg-laying. In the Trypetidae, the Agromyzidae, the Cecidomyiidae, and Drosophilidae, the ovipositor is elongate and adapted for

making holes and inserting the eggs in the leaves of the host. An unusually long ovipositor is found in a European form, *Phytomyza varipes* Meig., it being in this species as long as the abdomen.

The larvae. The larvae of the leaf-mining Diptera are very diverse. The more primitive forms are members of such families as the Tipulidae, and the Chironomidae, whose larvae have a definite head, with mandibles, maxillae, eyes, and antennae. The body is composed of a head, a thorax, and ten abdominal segments. The larvae of the leaf-mining species of these families resemble the free ranging forms in that they have a head of some sort, and mouth parts, but they differ in that they lack posterior breathing tubes, suckers, spines, and hairs. The projecting parts are reduced to a minimum. They show a reduction of protruding parts fitting them to their environment.

The larvae of the specialized families of leaf-miners, as the Anthomyiidae, the Trypetidae, the Drosophilidae, and the Agromyzidae, differ very little in structure from the larvae with other habits in these families. They are all highly specialized, with no head-capsule, mandibles, nor maxillae. The normal mouth parts are replaced by the pharyngeal skeleton. The antennae are reduced to minute, one-segmented appendages, and the eyes are absent. In certain of the leaf-mining families, the ambulatory setae are prominent structures.

The mines. The various kinds of mines produced by the Diptera can be classified under three types—linear, linear-blotch, and blotch. The long, narrow, and tortuous *linear mines* are undoubtedly the primitive type, and they occur chiefly in the primitive families, as Tipulidae. Only an occasional linear mine is found in the specialized family Agromyzidae, and none are found in the Anthomiidae. All blotch mines have their origin in a linear mine. As the larva enlarges its mine to form a blotch, the primary linear

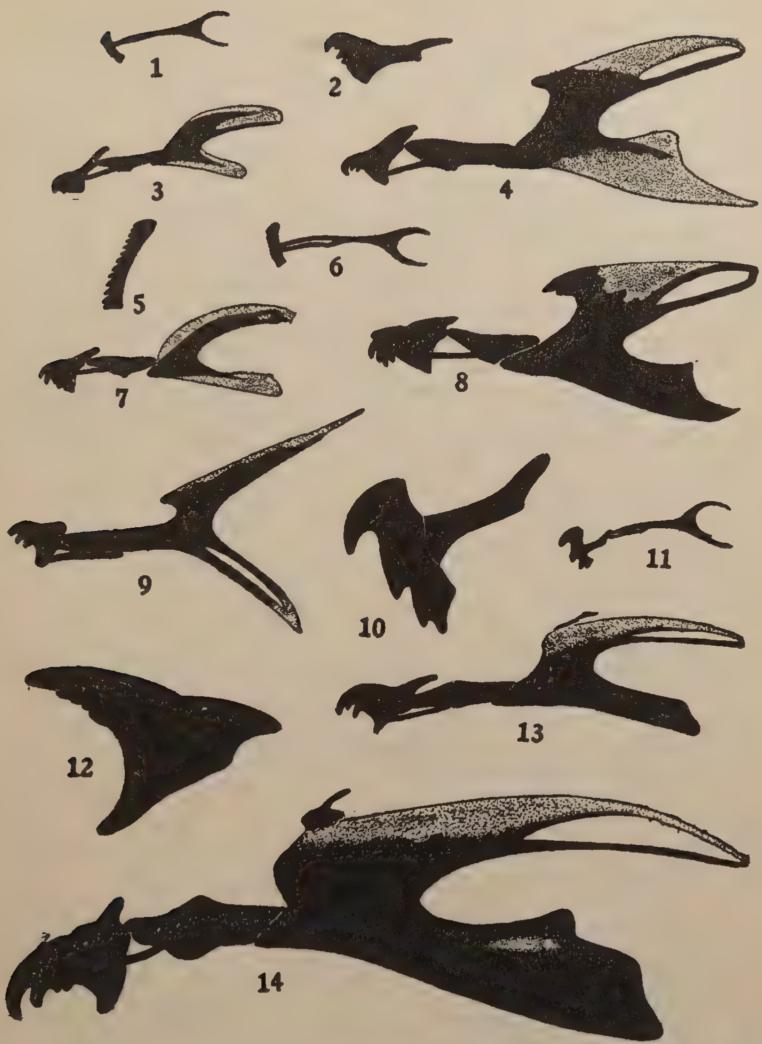


FIG. 70. Phryngeal skeletons and mouth hooks of Dipterous leaf-mining larvae. *1*, *Pegomyia calyptrata*, first instar; *2*, *4*, same, third instar; *3*, same, second instar; *5*, *Pegomyia vanduzeei*, first instar; *6*, mouth hooks in same; *7*, second instar; *8*, third instar; *9*, *Acidia heraclei; 10*, *Pegomyia hyoscyami*, first instar; *11*, mouth hooks in same; *12*, *Hylemyia fugax; 13*. *Pegomyia hyoscyami*, second instar; *14*, same, third instar.

mine is obscured. This primary mine is often very short, not more than an eighth to a quarter of an inch long. Some of the linear mines that are very narrow at the beginning and gradually enlarge, are called *serpentine mines*. Other mines are intermediate between the linear and the blotch types. The *linear-blotch mines* start as linear mines and suddenly change to the blotch type. They differ from the trumpet mines of the Lepidoptera in that the linear part does not enlarge gradually to form a blotch, but makes an abrupt connection with the enlarged part.

There is little difference between the blotch and the linear-blotch mine. In the former the primary linear mine becomes obscured by the blotch mine, while in the latter the original linear mine remains evident, and is usually of some length. The linear-blotch mines are produced by solitary miners. This perhaps explains their formation, since a single larva can mature in its mine without enlarging it sufficiently to cross the original linear tract and so obliterate it.

The mines can be further grouped according to their position on the leaf, the number of larvae within a mine, the arrangement of the frass, the position of the puparium, and the exit holes made by the larvae as they escape from the leaf.

Considerable variation is shown in the position of the mine on the leaf. The larvae of most species show a preference for the upper surface. A few species are found only on the lower surface. Some species, of which *Cerodonta femoralis*, *Agromyza parvicornis*, and *Agromyza laterella* are good examples, alternate between the upper and the lower surface of the leaf.

In a strict sense, most Dipterous leaf-miners are solitary, because they hatch from eggs laid singly on the surface or within the leaf, and as the larva emerges from the egg it must start its own mine. Since the eggs are often laid

adjacent to one another, the mines soon coalesce, and miners with such habits have, in the broad sense, been termed *gregarious.* All true linear miners are solitary. The blotch miners have both solitary and gregarious habits.

FIG. 71. Types of Dipterous mines. *1, Phytom. obscurella nigritella; 2, Agrom. curvipalpis; 3, Phytom. albiceps; 4, Agrom. pusilla; 5, Agrom. coronata; 6, Agrom. borealis; 7, Scaptomyza adusta; 8, Agrom. ulmi.*

The Anthomyiidae make large, blister-like mines, which frequently cover the entire leaf but seldom cause it to wilt. When the leaves are young and the plant is growing rapidly, the injury is entirely overcome. The Trypetidae, on the

other hand, make large, messy blotch mines in the leaves which wilt as a result of their attack.

The larvae of Agromyzidae affect the leaves in different ways. Some produce tortuous mines which at times make very beautiful patterns on the leaves. If these larvae become abundant they may kill the plant outright, especially if the mines are deep and large. The larvae that mine the thinner leaves cause them to wilt. If the mines are shallow, the growth of the leaf may not be affected. Some larvae cause a part of the leaf to wilt while the rest remains turgid, with the results that the leaf becomes distorted. Other species attack the unfolding leaves, giving them a wrinkled or fluted appearance. Such a condition is described under *Agromyza laterella.*

The frass. The arrangement of the frass in certain mines is very characteristic. In the mine of *Phytomyza nigritella* on peach and cherry, the frass is arranged in a distinct line of spots; no other dipterous or lepidopterous mine could be confused with it. The mine of *Phytomyza albiceps* bred from aster and goldenrod, has the frass in a prominent central line, resembling a lepidopterous mine in this respect; on other hosts, however, the mine of this species often has an indistinct frass line. In the remainder of the Diptera the frass is arranged in indistinct lines or is scattered about the mine.

The puparia. The position of the puparium has been found constant for each species. Most of the larvae, on maturing, cut a slit in the side of the mine, through which they escape. In some species the puparium is formed in the ground or beneath leaves or rubbish. In many species the larva transforms within the leaf and the puparium has a definite place in the mine. Some puparia are found loose within the mine, while others are attached to the upper or lower epidermis by means of a pellet of frass. Some are found in side channels to the main mine. These channels,

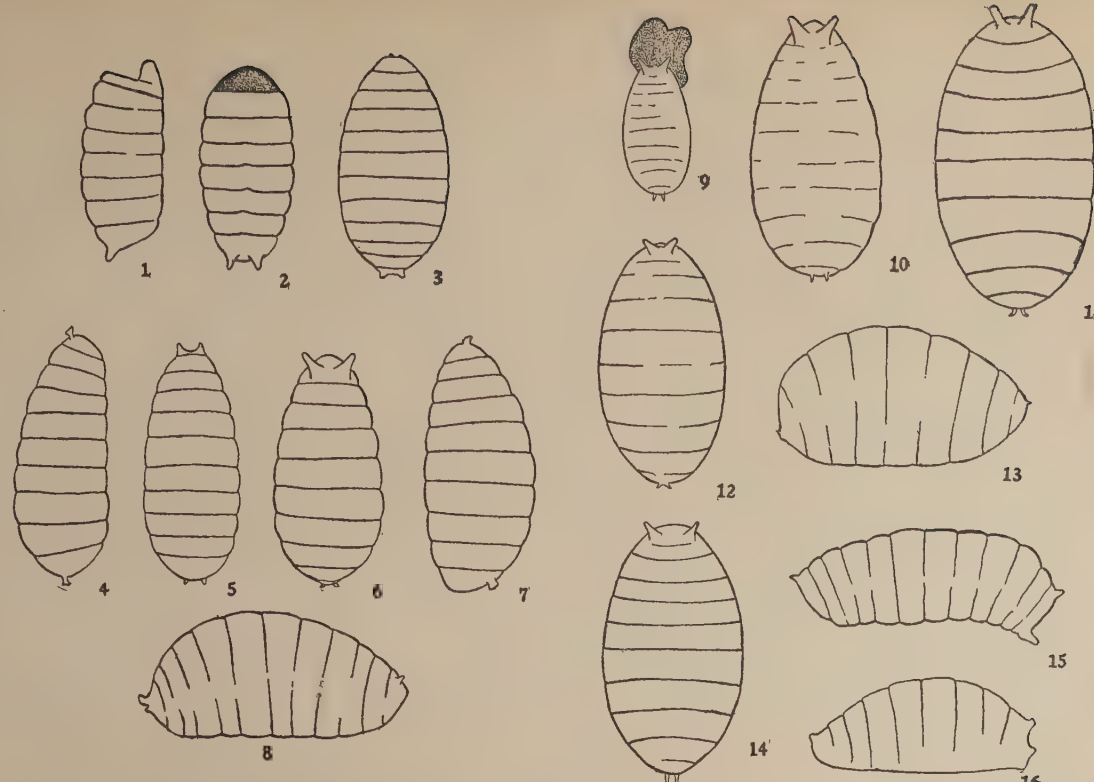


FIG. 72. Puparia of Dipterous leaf-miners. *1, Agrom. maculosa; 2,* same; *3, A. parvicornis; 4, A pusilla; 5,* same; *6, Phytom albiceps; 7,* same; *8, A. subnigripes; 9, A. cornata; 10,* same; *11, A. posticata; 12, A. melempyga; 13, A. subnigripes; 14,* miner on poplar; *15, A. allecta; 16, A. ulmi.*

which are evidently constructed for the purpose, may be found either on the same side of the leaf on which the mine occurs, or on the opposite side. Still other puparia are found with the puparial spiracles projecting through the epidermis of the leaf, and some protrude halfway from a slit made at the side of the mine. A few puparia are found attached to the exterior of the leaf, adjacent to the emergence hole. These would probably have fallen to the ground had they not been moist when they issued. Such puparia are often found rigidly attached to the outer surface of the leaf.

The exit holes made by the larvae in escaping from the leaf add further characters for classifying the mines. Many of the miners, especially those of the Anthomyiidae, make no definite exit holes but break through the parchment-like surface of their mines. The usual type of hole made by the other larvae is a small semicircular slit. The position of these holes varies according to the type of mine; in a blotch mine they are made at the side, and in the linear mine usually at the larger end. *Agromyza pusilla* Meig., when mining on nasturtium, usually retreats about a quarter of an inch from the end of its burrow and makes a slit parallel to the sides of the mines. As far as is known this is done by no other species.

Most of the Dipterous leaf-miners apparently pass the winter as puparia. This is particularly true in the three families Agromyzidae, Trypetidae and Anthomyiidae. In some instances the puparia remain in the leaves or in gall-like pockets until the following spring. In other instances the larvae fall to the ground and pupate beneath leaves or other rubbish, or penetrate the ground for a short distance.

Many of the species have several generations during the summer. Certain Agromyzidae have but a single generation.

In the Trypetidae and the Anthomyiidae, the adults feed on the surface of plant leaves, sucking up sweetened liquids

that have been deposited there by aphids or other insects. They also suck nectar from flowers. Some of the female Agromyzidae have a peculiar habit of making holes in the leaves with their ovipositors and then turning about and sucking the juice from the host.

A Key to the More Common North American Leaf-Mining Diptera, Based on Type of Mine Produced

1. Linear or serpentine mines, at least in part linear....................2
   Blotch mines, the linear part becoming obscured immediately.......17
2. True linear or serpentine mines..................................3
   Linear-blotch mines...15
3. Mines comparatively short, broad, seldom tortuous.................4
   Mines long and more or less tortuous............................10
4. Mines occurring on upper side of leaf, the larva escaping through a crescent-shaped slit...5
   Mines on lower side of leaf, or alternating from upper to lower side...6
5. Frass usually prominent, on Aster a prominent frass line, on *Symphoricarpos acemosus* and *Heracleum lanatum* not so prominent
   Phytomyza albiceps
   Frass not prominent, scattered; mine varying from linear to linear-blotch and blotch; occurring on a large number of host plants
   Agromyza pusilla
6. Mine on lower side of leaf, white, narrow at first, later becoming broad and almost blotch-like; frass in distinct spots; occurring on *Populus* species.................................An undescribed species
   Mine distinctly visible from both surfaces of leaf....................7
7. Mine very broad, almost a blotch..................................8
   Mine narrow, thread-like..9
8. Mine white, visible for its entire length from upper and lower side of leaf; occurring on *Smilacina racemosa*.......An undescribed species
   Mine alternating from upper to lower side of leaf, never visible from both sides at the same time..................*Agromyza parvicornis*
9. Mine deep, conspicuous, later becoming red in color, alternating from upper to lower side of leaf; occurring on grasses..*Cerodonta femoralis*
   Mine shallow, inconspicuous, white in color, alternating from upper to lower side of leaf; occurring on Iris...........*Agromyza laterella*
10. Mine with a conspicuous central dotted frass line
    Phytomyza obscurella var. *nigritella*
    Mine with or without a frass line, but never with a dotted frass line..11
11. Mine on under side of leaf, white in color; puparium formed in leaf; occurring on *Lactuca scariola* var. *integrata*. . . *Phytomyza lactuca*
    Mine on upper side of leaf...12

12. Puparium formed in mine, bulging from lower side of leaf *Agromyza curvipalpis*
Larva abandoning mine to transform..............................13
13. Mine white; no definite arrangement of frass, which is scattered in small spots; mine conspicuously tortuous, slightly visible from lower side of leaf; puparium usually attached to surface of leaf adjacent to exit hole..................................*Phytomyza aquilegiae*
Mine green or brown, not so tortuous as preceding; a double frass line 14
14. Mine green, with pale white edges; occurring on *Cornus circinata* An undescribed species
Mine brown, without pale edges; occurring on raspberry, strawberry, and blackberry...............................*Agromyza fragariae*
15. Script-like tracings preceding blotch part of mine..*Agromyza borealis*
No script-like tracings...16
16. Mine occurring on *Ulmus americana*................*Agromyza ulmi*
Mine occurring on *Philadelphus grandiflorus*.....*Agromyza melampyga*
17. Mine digitate; frass in spots at edge of mine.......*Scaptomyza adusta*
Mine a simple blotch..18
18. Mine large, messy, covering nearly the entire leaf.................19
Mine smaller, covering only a small part of the leaf.................21
19. Frass in small spots scattered about mine; mine occurring on parsnip and on *Cryptotaenia canadensis*..................*Acidia heraclei*
Frass soft, scattered about mine irregularly.......................20
20. Mine occurring on Rumex............*Pegomyia calyptrata, vanduzeei, bicolor, winthemi*
Mine occurring on Chenopodiaceae..............*Pegomyia hyoscyami, Hylemyia fugax*
21. Mine very small; puparium fastened within mine by a pellet of frass; occurring on Aster and Solidago..*Agromyza platyptera* var. *coronata*
Mine larger; puparium not fastened within mine as described above.22
22. A distinct white area around edge of mine; frass deposited in center of mine; occurring on *Thalictrum polygamum*...*Phytomyza plumiseta*
No white area about edge of mine.................................23
23. Mine showing distinct etchings in the form of semicircular cuts made by mouth hooks of larva.......................................24
Mine without such etchings......................................25
24. Mine occurring on *Helianthus annuus* and *Urtica gracilis*, *Agromyza reptans* var. *subnigripes*
Mine occurring on Aster and Solidago............*Agromyza posticata*
25. Mine on underside of leaf, occurring on Bidens, Arctium, and Eupatorium.......................................*Agromyza allecta*
Mine on upper side of leaf, occurring on *Camptosorus rhizophyllus* *Agromyza felti*

THE LEAF-MINING GENERA OF DIPTERA §

FAMILY	GENERA	DISTRIBUTION	NUMBER OF DESCRIBED SPECIES†	NUMBER OF MINING SPECIES
Tipulidae	*Dicranomyia	Hawaii	25	1
Chironomidae	Cricotopus	N. A.	21	Not true leaf-miners
	Chironomus		203	
Cecidomyiidae	Monarthropalpus	N. A.	1	1
Trypetidae	Acidia	N. A., Eur.	5	4
	*Oxyna	Eur.	30	1
	*Spilographa	Eur.	8	2
Agromyzidae	Agromyza	N. A., Eur. N. Z. Africa	175	111
	Phytomyza	N. A. Eur. N. Z.	115	80
	Cerodonta	N. A. Eur.	9	1
	Napomyza	N. A., Eur.	?	3
Drosophilidae	Scaptomyza	N. A., Eur.	7	6
Ephydridae	Hydrellia		55	10
	Notiphila		25	1
Anthomyiidae	*Chirosia	Eur.	7	2
	Pegomyia	N. A., Eur.	109	16
	‡Hylemyia	N. A., Eur.	282	8
Cordyluridae	Parallelomma	N. A., Eur.	7	6

* Exotic.

† According to Beeker, Bezzi, Kertesz and Stein, 1903–1907.

‡ The genera Chortophila and Hylemyia combined.

§ From Frost, 1924.

The families comprising the leaf-miners of the order Diptera are relatively few in number. Only eight of the sixty-two families listed by Williston (1908) have leaf-mining genera. These are given in the synopsis on page 241.

FAMILY TIPULIDAE

Crane flies

In this large family there is as yet but a single known leaf-mining species, *Dicranomyia foliocuniculator*. Swezey, reared it from the leaves of *Cyrtandra paludosa* in the mountains at Punaluu in the Hawaiian Islands. He states (1913) that the larvae make linear mines on the leaves and pupate within the mine. His figure of mine and developmental stages, we copy herewith.

FAMILY CECIDOMYIIDAE

Gall midges

This family contains, in our fauna so far as known only one well-defined leaf-mining form, and another that combines mining with gall making. These represent the two genera discussed below.

Monarthropalpus

The boxwood leaf-miner has undoubtedly been introduced from Europe. It infests ornamental hedges of its host plant, damaging the appearance of the leaves. The first indication of the mine appears as a small yellowish or greenish spot on the upper surface of the leaf. Opposite this, on the under side of the leaf, can be seen an irregular blister, caused by the maggot enlarging its mine. Later the injury becomes more pronounced, and a slight elevation, with a yellowish or brownish discoloration, is seen on the upper surface of the leaf. The larvae pass the winter in these gall-like pockets, and in the spring transform to light orange-

FIG. 73. *Dicranomyia foliocuniculator*. *1*, larva; *2*, puparium; *3*, venation; *4*, leaf of Cyrtandra showing mines. (After Swezey.)

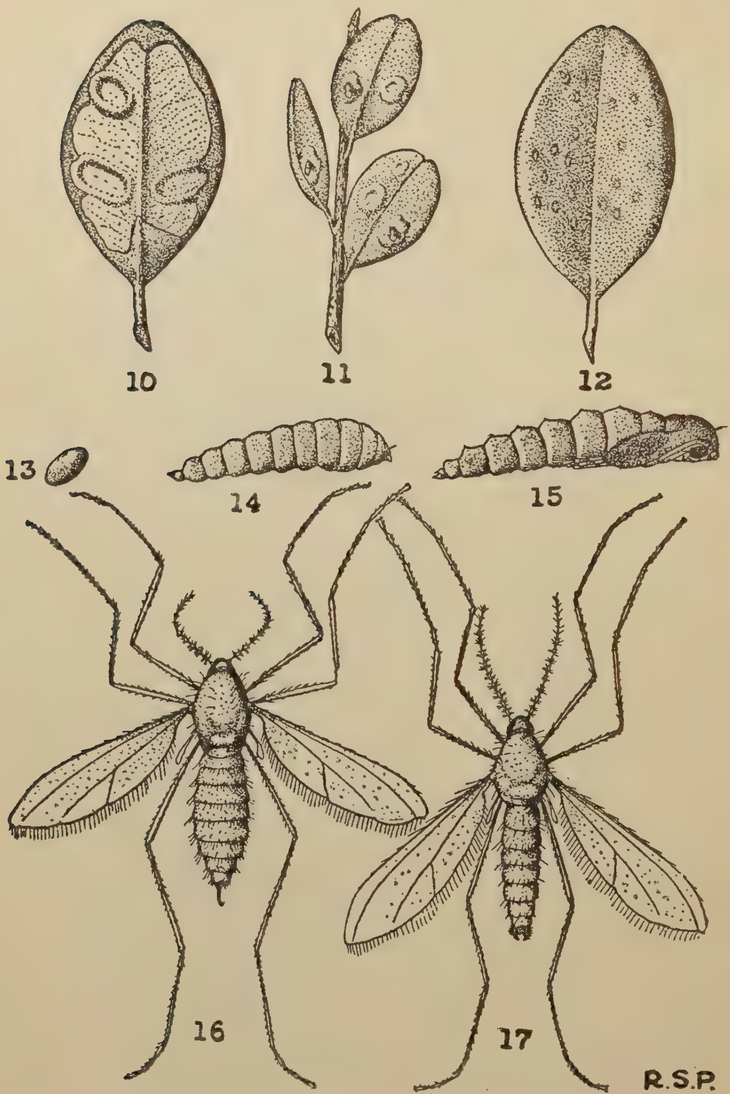


FIG. 74. *Monarthropalpus buxi.* *10,* boxwood leaf, surface removed showing mines; *11,* boxwood leaf showing galls; *12,* eggs on leaf; *13,* egg; *14,* larva; *15,* pupa; *16–17,* adults. (After Weiss.)

colored pupae within the leaf. An infested leaf may contain twelve or more larvae.

The European boxwood is apparently the only food plant of the species. It is commonly imported from England, France, and Holland. Inspectors from Washington, D. C., and from various places in New Jersey and New York, have intercepted the miner in making examinations of imported stock.

Thecodiplosis

This genus includes a species, *T. liriodendri* O. S., which has been called a leaf-miner by Osten Sacken but has been included by other authorities among the gall-makers. The distinction here between the mining and the gall-making habit is a matter of interpretation (see p. 23). The larva appears at first to cause a gall to grow and then mines out the center of it. The leaf becomes spotted with brown capsule-like dots 2 to 3 mm. in diameter plainly visible from either side, each surrounded by a broader ring of green or yellow or tan. The larva lives within the central area and consumes its mesophyl.

Family Trypetidae

There is known in our fauna in this family but a single leaf-mining species, *Acidia heraclei*. It is widely distributed in Europe and in America where it infests the leaves of a number of herbs.

The larvae produce irregular blotch mines. Several larvae work within a single mine, thereby making it very large. The epidermal layers of the leaf become separated, forming a large pocket within the leaf, which is often filled with considerable moisture and contains blackish frass scattered about in small spots. This gives the mine a very dilapidated and messy appearance. As the mine dries, it becomes brownish in color and the leaf curls as though it

had been burned by spray material or by the sun. The mature larvae frequently transform within the mine, although they may escape and attach themselves to the surface of the leaf or hide away in a curled part of it.

AGROMYZIDAE

This is a family of small flies, the habits of many of which are still unknown. The larvae seem to be largely plant

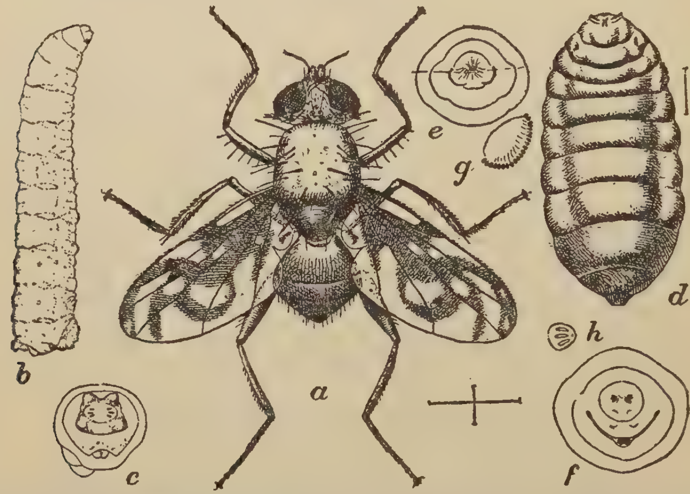


FIG. 75. The parsnip leaf-miner, *Acidia heraclei*. *a*, adult; *b*, larva; *c*, *f*, *h*, details of larva; *d*, puparium; *e*, details of puparium. (From Chittenden.)

feeders, and the majority are leaf-miners, stem borers or gall producers. The leaf-mining forms occur in four genera; Agromyza, Phytomyza, Cerodonta and Napomyza. There are approximately 194 species which mine leaves. Many of them are European species.

The egg. The eggs of this family are soft, white and smooth, and vary in form from broadly oval to sub-cylindrical. All, as far as known, are inserted within the tissues of the leaf.

The larva. The larvae are soft, white, headless, legless, maggots, as in other families of the higher Diptera, with two pairs of spiracles one pair anterior and one posterior; and with only a pair of cell-tearing mouth-hooks for feeding tools.

The larvae of Agromyzidae have three types of anterior spiracles—fan-shaped, semicircular, and forked. The first two types are the commonest. In Phytomyza the anterior spiracles tend to be approximated at the base, and project rather prominently. Certain of the species have very characteristic spiracles. In *Phytomyza nigritella*, for example, the anterior spiracle is forked and has about twenty-six stigmatal openings.

The posterior spiracles in this family are even more varied in form than the anterior spiracles. The number of stigmatal openings resemble those of Pegomyia. The stigmatal openings, where few in number, are arranged either subparallel or radiating from a central point. The spiracles with a larger number of stigmatal openings have various forms, which are usually very characteristic of the species in which they are found.

It is not always easy to distinquish between the mouth hooks of different species. The number of teeth varies from two to four. In most species these sclerites are quadrangular in shape. Often they are unequal in size, the left one being the smaller. In one species, *Agromyza laterella*, they are triangular and have sharp teeth, somewhat resembling those in pegomyia.

The ambulatory setulae are minute chitinized hooks which encircle the edges of the segments in transverse bands. They serve as a means of distinguishing Agromyza from Phytomyza. In Agromyza they are almost always prominent, while in Phytomyza they are either absent or exceedingly minute.

None of the Agromyzidae have prominent tubercles such as are found in Authomyiidae. Some species of Agromyza

have small tubercles on the lateral aspect of the last segment. There are two lateral tubercles in *A. parvicornis*, and one in *A. melampyga.* No tubercles have been found in Phytomyza.

The pupa. The pupa is formed inside the hardened larval skin or puparium, and this turns brown or black, as usual, but shows distinct and rather deep intersegmental constrictions along the sides, with anterior and posterior spiracles projecting at the ends.

The adult. The adults are small blackish or yellow marked clearwinged flies generally a quarter of an inch or less in expanse of wings, as shown by our table on page 241, this family contains the bulk of the leaf-mining species of Diptera.

The females of certain Agromyzidae have a peculiar way of puncturing the leaves of the host and feeding on the juices. One of us (Frost) has observed this in several species of the genera Agromyza and Phytomyza. It may be that all of the Agromyzidae feed in this manner, but it has been observed in only a few species. The ovipositor is elongated and is especally adapted for inserting the eggs within the tissues of the leaf, but it serves equally well in making feeding punctures. After making a puncture in the leaf, the female turns about and sucks the juice through the hole. The feeding punctures are usually large and very conspicuous. Some species, however, make very small punctures which resemble the feeding punctures of mites or thrips.

Some species of Agromyzidae issue from their winter quarters in spring, as early as April or by the first of May. Others do not appear until June or July. Several species have but one generation a year, and this appears in the spring. It is impossible to obtain either larvae or adults of these species toward the middle of summer. Other species have several generations, and are active throughout the entire summer. These keep the leaves continually covered with fresh mines.

AGROMYZA[1]

This is the largest genus of leaf-mining Diptera. Its members are all plant-feeders; most of them are leaf-miners but some mine beneath the bark, a few produce galls and some are stem borers. *Agromyza pruinosa*, A. *aceris*, and A. *amelanchieris* are cambium miners; A. *tiliae*, A. *schineri*, and A. *websteri*, are gall-producing forms; A. *aeneiventris*, A. *simplex*, and *A. virens*, are stem-mining forms; the remaining species of this genus, as far as their habits are known, are leaf-miners.

Our present knowledge of the biology of the North American species has been summarized by one of us, Frost (1923) and his key for the determination of the known North American larvae is reproduced herewith:

Key to the Leaf-Mining Larvae Agromyza

1. Last abdominal segment with two fleshy lobes projecting from ventral posterior angle, resembling prolegs........................*allecta*
   Last abdominal segment without fleshy lobes........................2
2. Posterior stigmatal slits on curved horny projections at posterior end of body........................3
   Posterior stigmatal slits at ends of short or long peduncles............4
3. Ventral edge of second segment produced into two fleshy lobes *angulata*
   Ventral edge of second segment not produced................*borealis*
4. Posterior spiracles with three stigmatal slits........................5
   Posterior spiracles with more than three stigmatal slits...............9
5. Posterior spiracles fan-shaped, with stigmatal slits at end of separate lobes; mouth hooks triangular, with 4 teeth................*laterella*
   Posterior spiracles with slits on stigmatal plates.....................6
6. Posterior spiracles with stigmatal slits subparallel.........*subnigripes*
   Posterior spiracles with stigmatal slits arranged radiately............7
7. Teeth of mouth hooks exceptionally long..................*fragariae*
   Teeth of mouth hooks normal........................8
8. Peduncle of the posterior spiracle long....................*posticata*
   Peduncle of the posterior spiracle short..................*coronata*
9. Mouth hooks with four teeth..........................*melampyga*
   Mouth hooks with two teeth................*pusilla* and *parvicornis*

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[1] This genus has been split by European workers into six genera: Domomyza, Ophiomyia, Melanagromyza, Haplomyza, Dizygomyza and Liriomyza.

A few common species with vary characteristic mines have been selected to illustrate something of the range of the habits of this genus.

The syringa or mock orange leaf-miner (*Agromyza melampyga* Loew can be determined by its mine and host plant. The eggs are deposited under the upper epidermis usually some distance from the edge of the leaf. The larva makes at first a relatively long linear mine. Later the mine expands

Fig. 76. Mine of *Agromyza melampyga* on syringa.

into a small blotch about three quarters of an inch or an inch long and about half as wide. The frass is laid down in two broken lines, one on each side of the mine. In the blotch portion of the mine the frass tends to become somewhat scattered although the double line of frass can be followed. These mines are not at all visible from the lower side of the leaf. They are pale green in color or even whitish. When mature the larva cuts a slit usually in the upper epidermis and escapes form its puparium.

The serpentine leaf-miner (*Agromyza pusilla*) is the commonest and possibly the most widely distributed species of

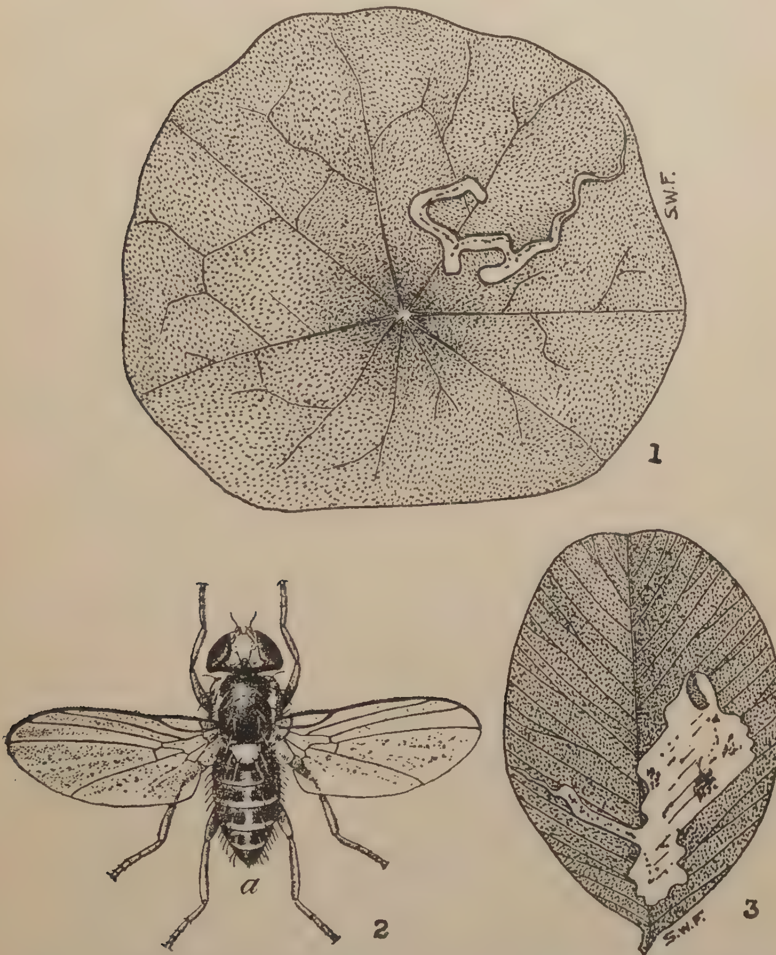

Fig. 77. The serpentine leaf-miner, *Agromyza pusilla*. *1*, mine on nasturtium (original); *2*, adult (after Webster and Parks); *3*, mine on clover. (original).

this family. It is a general feeder and has a great variety of hosts, mining at least fifty-five species of plants. An excel-

lent life history study of this miner may be found in Webster and Parks (1913), from which we have taken our account.

The female inserts her eggs beneath the upper epidermis. They are pale, white, oval, about 0.25 mm. long and can frequently be seen through the upper epidermis. The larvae commence feeding immediately after hatching. The mine is at first very small and thread-like gradually widening with the growth of the larva. The larva is not able to enter a fresh leaf and must obtain its nourishment from a single leaf. The mine is typically linear, considerably curved but never greatly elongate. Often, however, a blotch is produced on the leaf. Frost (1923) mentioned its peculiar habits when mining the leaves of Nasturtium. The mines on nasturtium are always short and of the linear or serpentine type. Seldom more than one or two mines are found on a single leaf. When full grown the larva invariably retreats a short distance from the end of its mine and makes a slit parallel with the sides of the mine through which it escapes.

Webster and Parks tells us that the number of generations depend upon latitude and seasonal conditions. In North Indiana during the season of 1912 there were six generations. The larvae may transform within their mines or escape as mentioned above and form their puparia outside their mines. Apparently in arid and semi-arid regions the larvae transform within their mines while in humid sections they abandon their mines to transform. In Florida the larvae may continue their feeding throughout the winter. Even in Arizona in mild winters larvae have been found mining in the leaves until Christmas. The larvae apparently feed until cold weather prevents their activities and naturally large numbers are killed by the cold and never transform.

The two winged elm leaf-miner, *Agromyza ulmi* Frost, is abundant in New York and Pennsylvania. It is an interesting leaf-miner because it is one of the few Diptera which mine the leaves of woody plants.

The adults emerge from their overwintering puparia very early in the spring. Hardly have the new leaves opened than these flies can be seen flying about the elms. The eggs are minute and difficult to find. They are inserted beneath the upper epidermis usually at or close to the margin of the leaf. The larva mines towards the center of the leaf making a narrow linear track which is pale green in color. During this time the larva moults twice leaving their mouth hooks and larval skins behind to tell the tale. After the second

FIG. 78. Mine of Agromyza ulmi on American elm.

moult the mind is broadened to form a blotch about an inch in length. The blotched portion of the mine is brown in color and within can be seen the frass arranged in two more or less regular rows of dots. The swaths made by the larva in getting its food is feebly impressed on the parenchyma of the leaf. When mature the larva escapes through a semicircular slit cut either in the upper or lower surface of the mine and the larva falls to the ground where it forms its puparium.

There is apparently but one generation a year and this

occurs early in the season. By the middle of May the mines become very noticeable upon the lower leaves of the elms. In the course of a couple of weeks it is almost impossible to find a larva as all have transformed. Some difficulty has been experienced in rearing this species and this is probably due to the fact that the majority of the puparia remain dormant during the summer and adults do not emerge

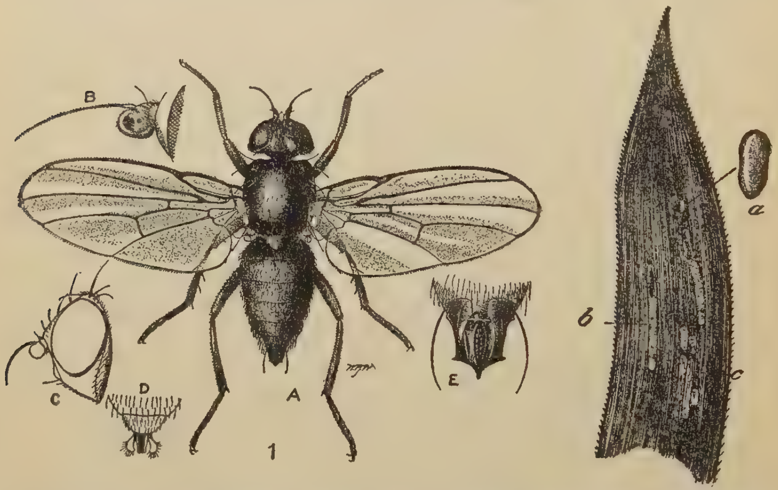

FIG. 79. The corn blotch leaf-miner *Agromyza parvicornis*. *A*, dorsal view of adult; *B*, antenna ♀; *C*, head of ♂; *D*, hypopygium of ♂; *E*, Ovipositor. *a*, egg; *b*, newly hatched larva in mine; *c*, feeding punctures of adults. (From Phillips.)

until the following spring. A few flies have been secured from puparia which transformed in the early spring.

The corn-blotch leaf-miner (*Agromyza parvicornis*) mines several species of grasses of which wheat and corn are the most important. It is apparently indigenous to North America, now having a wide distribution over the United States. It can safely be called a common species.

Phillips (1914) has studied the life history of this leaf-miner and we take our account from his investigations.

The egg is milky white and flattened from above and below. It is broadly rounded at each extremity and slightly constricted at the middle. It is from 0.45 to 0.50 mm. long. These are deposited under the upper or lower epidermis of the leaf. They are usually placed at the tips of the leaves. The feeding punctures and the egg laying punctures of the female are similar. In making the puncture the fly forces the point of her abdomen downward rearing the anterior portion of her body slightly and touching the tip of the abdomen to the leaf, whereupon the small lancets, which apparently make up the ovipositor are put in motion. They are forced down between the two surfaces of the leaf and a strip of the epidermis about 0.3 mm. in width and about 0.9 mm. long is pushed back. The egg is then inserted and the flap is in some way brought back over the egg and fastened probably with a mucilagenous substance.

The larva mines towards the base of the leaf forming a broad linear or sometimes a blotch mine. This may alternate from the upper to the lower side of the leaf. The larva cannot enter a new leaf and must mature within the leaf on which the egg was laid. The larvae are gregarious, several mines unite bringing the larvae in a common mine. There are possibly four or five broods in this latitude. When mature the larvae escape and transform outside the leaf. They hibernate as puparia.

The iris leaf-miner (*Agromyza laterella* Zett.). This unique leaf-mining and gall-forming species has been studied in some detail by Claassen (1918). We take the following account from his studies.

The flies emerge the latter part of May from their overwintering galls. The female inserts her eggs into the tissues of the leaf causing rather conspicuous abrasions. When the eggs hatch delicate mines are formed on the innermost leaves. The mines are at first so delicate to be hardly perceptible to the naked eye. The mine is linear enlarging

as the larva proceeds downward and increases in size. Frequently the larva suddenly changes to the opposite side of the leaf so that the mine is no longer visible on the upper surface, thus presenting a broken appearance. The color of the mine is white and shows plainly on the green leaf es-

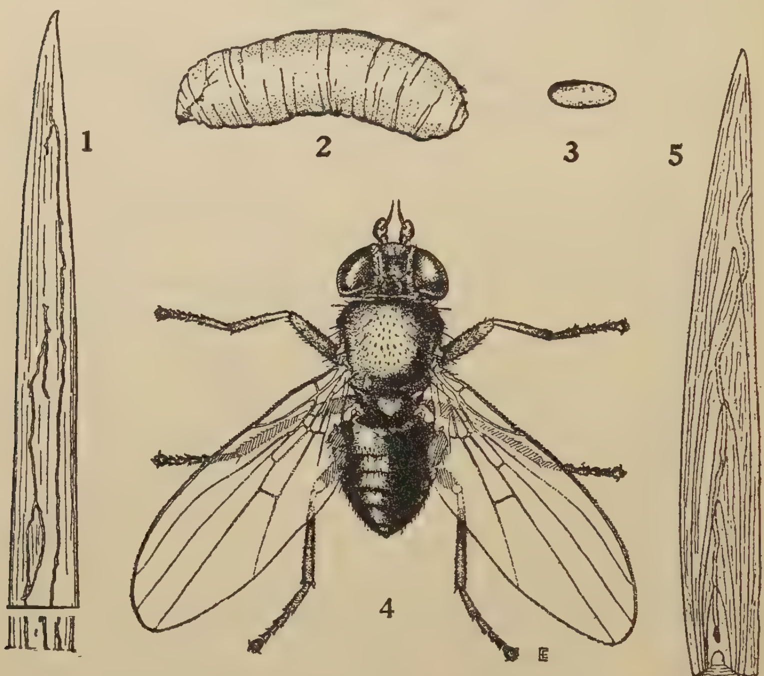

Fig. 80. The iris leaf-miner, *Agromyza laterella*. *1*, outer leaf of iris showing the characteristic mines made by the larvae; *2*, full grown larva; *3*, egg; *4*, adult ♀; *5*, leaf bundle cut to show the course of the larva as it mines down towards the new forming leaf. (After Claassen.)

pecially on the lower part of the leaf, which in the iris, is of a purplish color. The larva proceeds downward just about as rapidly as the new leaves are formed and comes out of the leaf bundles and pass on, thus being in a situation where the tissue is newest and most tender. Sometimes, however, the larva may remain in an outer leaf and mine the entire

length of it. When the larvae reach maturity in early or mid-summer, the puparia were always formed at the base of one of the larger outer leaves. A somewhat enlarged excavation is made, and here transformation occurs. The base of the leaf around the puparium swells just a little, thus showing a slight tendency towards gall formation.

The larvae in the fall are always found mining on the innermost leaves of the bundle. Just as the plant ceases growth before winter sets in the larva enters and transforms into a puparium.

Fig. 81. Mine of *Agromyza borealis* on jewel-weed.

In the spring when the plant resumes its growth, it is the little leaf in the center which contains the puparium, that causes the characteristic gall. Probably not over 20 to 25 per cent of the larvae enter the inner leaf and form galls.

The jewelweed leaf-miner (*Agromyza borealis* Mall.) may be found abundantly in moist or wet locations. These flies have selected one of the thinnest of leaves to mine. Although the leaves are thin and the plant very succulent, wilting readily when plucked, the miners do not seem to affect the leaves in any way except to make their characteristic linear-blotch mines.

The adults are marked with considerable yellow and when resting in the sunshine glisten like gold. They have a

peculiar habit of hovering like syrphus flies before alighting. The females further have a habit of puncturing the leaves with their ovipositors and turning about and sucking the juice with their mouths. It is a common sight to see leaves covered with these small feeding punctures.

The eggs are laid in the tissue of the leaf, probably from the upper side. The larvae are solitary miners although several may be found within a single leaf. The mine is at first linear, turning and twisting considerably and often threadlike. Later it expands into a blotch. When several larvae mine on a single leaf the mines anastomose so that it is difficult to trace the course of the mines. The frass occurs in a broken line down the center of the mine becoming somewhat scattered in the blotched portion of the mine. When the larve is mature it cuts a slit at the edge of the mine through which it escapes. The puparium is formed outside the mine. There is probably only one generation during the summer.

NAPOMYZA

Of the few European species included in this genus one *N. lateralis*[2] may occur as a leaf miner in the sowthistle, *Sonchus oleraceus*, in North America. It has been little studied. The best account of it is the brief one that was published by Goreau in 1851. He said that the larva makes a filiform curving mine, which gradually widens from its origin; that it is solitary, that it grows rapidly and is common; that it finally comes to rest against the lower epidermis of the leaf where it changes to a yellowish puparium.

CERODONTA

A single leaf-mining species, *C. femoralis*, infests the leaves of corn and other grains and grasses. It was called the corn

[2] The early records of *P. lateralis* Fall in this country are referable to *Phytomyza chrysanthemi* Kowarz.

leaf-miner by Britton (1895) and the spike-horned leaf-miner by Luginbill and Urbans (1916), whose figures we copy and whose account of its habits we abstract.

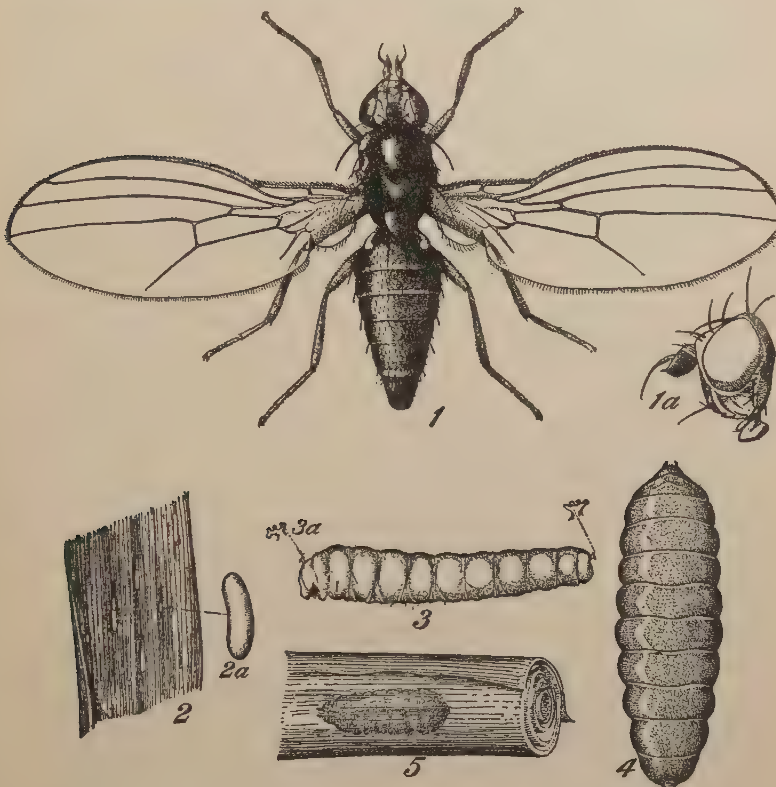

FIG. 82. The spike-horned leaf-miner, *Cerodonta femoralis*. *1*, adult ♀; *1a*, head of same; *2*, leaf-blade showing egg in situ; *2a*, an egg greatly enlarged; *3*, larva, enlarged; *4*, puparium, dorsal view; *5*, section of barley stem, showing usual position of puparium beneath the sheath. (From Luginbill.)

The female fly selects a suitable place for oviposition, usually near the tip of the leaf or along the edge. With head elevated and tip of abdomen lowered, the body is held almost perpendicular to the leaf surface, and by rapid pierc-

ing movements of the abdomen the epidermal leaf tissue is punctured. The ovipositor is then forced by repeated thrusts to its full length between the upper and lower layers of the leaf, the egg quickly deposited, and the ovipositor withdrawn to its normal position. Only one egg is deposited in a puncture, but the fly repeats the process of oviposition a number of times in a given day. Frequently she oviposits into what are apparently small feeding punctures.

Eggs may be deposited either from the upper or lower side of the leaves, but the majority of them are deposited from the upper side. They are placed with the longer axis of the egg parallel to the veins of the leaves.

The larva, when ready to emerge, ruptures the cephalic end of the egg shell and immediately begins to feed on the green tissues of the leaf. The mine at first is very small and threadlike, scarcely noticeable to the unaided eye. The diameter of the mine increases as the larva increases in size, and by the time the larva reaches maturity the mine may be greatly widened. In large plants, with long, wide leaves, the larvae frequently makes mines from 15 to 20 inches in length. Such mines are usually linear in outline, and although they run from side to side, the turns are less frequent than when larvae mine in short leaves of smaller plants. In the latter the larvae traverse the leaves oftener. They frequently make side galleries diagonally across the leaves, then retreat and continue the main mine down the blade. A number of these galleries are often found leading away from one mine in a leaf. All sorts of peculiarly shaped mines are made in leaves, especially in small plants or in plants with a limited amount of leaf surface. Some of these mines show almost perfect loops, while others traverse the leaves in snakelike fashion.

In young oats and barley the larvae apparently break away from the accustomed habit of making thread-like mines and instead appear to undermine almost the entire upper

surface of the leaves in which they are feeding. As a result the leaves dry up.

The larvae of this species pupate in the mines, usually in the leaf sheath. The adult, upon emerging from the puparium, tears open the dry tissue at or near the pupal case and makes its escape.

PHYTOMYZA*

This is in number of species the second largest genus of leaf-mining species among the Diptera. The larvae of this genus, are largely leaf-miners. It is the only genus among the Diptera that forms a natural group with such a habit. The food plants of most of the species are already known. The smooth larvae make mostly linear or serpentine mines on a variety of plants; and the plants mined may differ in their leaves as greatly as do Impatiens and thick-leaved hollys. The white tracery of the columbine miner, *P. aquilegiae,* on leaves of Aquilegia is familiar to everyone.

Key to the Larvae of Phytomyza

1. Anterior spiracles distinctly bifurcated.................... *nigritella*
   Anterior spiracles fan-shaped or semicircular, but not bifurcated.....2
2. Mouth hooks with 2 or 3 teeth..................................3
   Mouth hooks with 4 teeth......................................7
3. Mouth hooks with 2 teeth......................................4
   Mouth hooks with 3 teeth......................................6
4. A tentacle on dorsum of first segment.................... *aquifolii*
   No tentacle on first segment..................................5
5. Posterior spiracles semicircular, with 22 stigmatal slits....... *plumiseta*
   Posterior spiracles semicircular, with 8 or 9 stigmatal slits.. *plantaginis*
6. Posterior spiracle with 15 to 18 stigmatal slits.............. *albiceps*
   Posterior spiracle with 9 stigmatal slits, peduncle of medium length *chrysanthemi*
7. Anterior spiracles with 9 stigmatal slits...................... *ilicis*
   Anterior spiracles with 26 stigmatal slits................. *nigritella*

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* The identity of some of these species especially *P. aquilegiae* Hardy, *P. ilicis* Curtis, and *P. aquifolli* are in dispute. No attempt is made to straighten synonymy here.

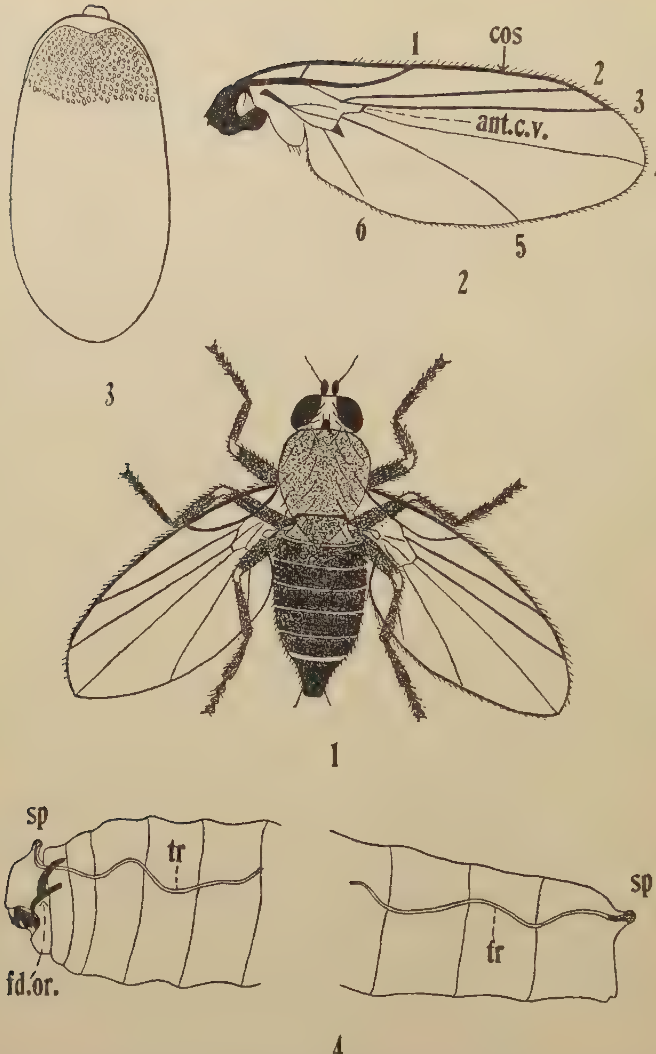

FIG. 83. The chrysanthemum leaf-miner, *Phytomyza chrysanthemi*. *1*, adult; *2*, wing; *3*, egg; *4*, larva. (After Smulyan.)

Perhaps the best known species in this family is the chrysanthemum miner, *P. chrysanthemi*, which has been most carefully studied by Smulyan (1914). It is a serious greenhouse pest. It damages chrysanthemums, marquerites, few ferns, and related compositae, by puncturing and mining the leaves.

The adult is a small grayish fly, hardly a sixth of an inch (4 mm.) in expanse of wings, being a yellowish color along each side of the abdomen. It may be found resting on the leaves of its host plant, or "crawling lazily about or making its way from plant to plant in a skipping or hopping flight. The eggs are laid simply in horizontal incisions made by the ovipositor between the parenchyma or flesh and epidermis or skin of the leaf."

The egg punctures are in the lower surface; but the larva or hatching soon passes to the upper or palisade layer of the mesophyl and mines just beneath the upper epidermis, excavating an irregularly linear, often zigzagged and intercrossing tract, that is whittish in color and stands out prominently on the green leaf.

The mine is gradually widened and at the last it is deepened also to form a cavity in which pupation takes place. The boat shaped puparium is visible through the transparent epidermis. Ordinarily only the minute anterior spiracles are protruded through the epidermis.

Smulyan's (1914) seasonal notes on the mean life cycle are as follows:

	days
Time elapsing between emergence of adult and oviposition....	$1\frac{1}{2}$
Length of egg stage....	5
Length of larval stages....	13
Length of papal stage....	14
Average length of one generation....	$33\frac{1}{2}$

The wild lettuce leaf miner (*Phytomyza lactuca* Frost) is common and has been found wherever the lettuce occurs

in New York and Pennsylvania. The eggs are inserted under the lower epidermis and the mines are confined to the lower surface of the leaf. Although the mines may be abundant they are easily overlooked because they are not at all visible from the upper side of the leaf. The mines are shallow, linear, very elongate and often anastomosing considerably to form small blotches or lateral chambers. They are pure white in color, the width of the mine changing very little during its course. The larva transforms at a slightly enlarged chamber at the end of the mine.

FIG. 84. Mine of *Phytomyza lactuca* on wild-lettuce.

The Columbine leaf-miner, *Phytomyza aquilegiae*, is a common species about Ithaca, New York, and frequently is injurious both in greenhouses and in flower gardens.

Cory (1916) has some excellent notes on the eggs of this species which we borrow.

> The egg is oblong-oval, slightly longer at one end. It is translucent pale greenish white sub-glossy and bears no surface markings. Length 123. × 235 microns.
>
> The eggs are deposited in the under side of the leaves with the point sometimes directed almost at 90 degrees to the leaf surface and again they may be pushed into the tissues so far that they lie parallel with the leaf surfaces.

The larvae[3] produce very conspicuous and rather beautiful, long, linear mines. These occur only on the upper side of

[3] The following account has been taken from Frost (1924).

the leaf, although the comparative thinness of the leaf makes them slightly visible from the lower surface also. The mines are whitish in color and the frass is scattered in small spots and is not conspicuous. Sometimes the larvae produce blotch mines. European workers refer to this species as a blotch-miner.

The full grown larvae abandon their mines to transform. They make their exit through a semicircular slit at the end of the mine, on the under surface of the leaf. The puparia are exceptionally small, football-shaped, dark colored and look very much like seeds.

The adults, like many of the agromyzidae, make circular punctures in the leaves with their ovipositors and through these punctures they suck the juices of the plant. The punctures later become whitish in color, and are as conspicuous as the mines themselves.

DROSOPHILIDAE

The small flies of this family are closely related to the Agromyzidae and the Ephydridae. The leaf-mining species are yellowish or light colored and the bristles of the front are conspicuous. The larvae of the Drosophilidae are mostly scavengers feeding on decaying or fermenting fruits, vegetables or other refuse. The appearance of the leaf-mining habit in this family is unusual and represents a habit that is not entirely established. While some of the species have adapted themselves to the leaf-mining habit, they can also be bred through several generations on tomato fruits or potato tubers showing that they have not entirely departed from their scavenger habits. The leaf-mining species belong to the genus Scaptomyza.

Scaptomyza

The species of this genus have been badly mixed up in literature. There are apparently three North American

leaf-mining species. These have been designated as the Imported turnip leaf-miner (*Scaptomyza flaveola* Meig.), the Imported cabbage leaf-miner (*Scaptomyza graminum* Fall.[4]), and the Native cabbage leaf-miner (*Scaptomyza adusta* Loew.). Another species *Scaptomyza terminalis* Loew., may prove to be a leaf-mining form. Sturtevant (1921) believes that *S. flaveola* Meig., does not occur in America stating that this species is referable to *S. adusta* or *S. graminum*.

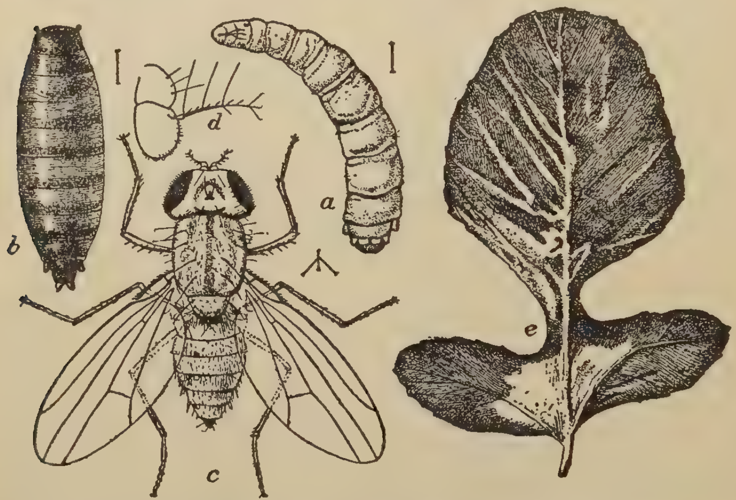

FIG. 85. The turnip leaf-miner, *Scaptomyza flaveola*. *a*, larva; *b*, puparium; *c*, adult; *d*, antenna; *e*, mined leaf. (From Chittenden.)

The native cabbage leaf-miner *Scaptomyza adusta* Loew., is common in New York State. It mines chiefly in the leaves of the cruciferae although pea and a few other plants are attacked. The adults occur abundantly during the summer and are frequently taken by sweeping fields or roadsides with a net.

[4] Duda 1921 proposed a new name, *S. disticha* for this species.

The eggs are laid on the surface of the leaf and the young maggots eat their way into the interior of the leaf where they form their mine. The larvae are gregarious. Twenty-eight larvae have been found within a single leaf of garden pea. They produce small irregular blotch mines usually on

FIG. 86. The cabbage leaf-miner, *Scaptomyza adusta*. *1*, larva; *2*, mine on young cabbage leaf.

the upper side of the leaf, close to the mid rib, mining the veins as well as the leaf itself. The mine is often digitate with finger like projections in which the frass is deposited. Pupation takes place within the mine. The larvae may mine down the petiole and transform there. There are

two or three generations during the summer. The last generation emerges during September and October and these adults apparently hibernate.

EPHYDRIDAE

The flies of this family frequent moist or aquatic locations. They are blackish or metallic in color with widly separated eyes and few bristles upon the head. Their close relationship with the Agromyzidae and the Drosophilidae has already been pointed out.

The larvae live in wet situations, many inhabiting salt water or even brine. Some have been found feeding in the sap of trees, others boring in the stems of plants and the species of the genera Hydrellia and Notiphila mine the leaves of plants. The food plants listed by Frost (1923) would indicate that grasses formed their favorite host plants but the recent work of Hering (1925) shows that many aquatic plants of the European genera Alisma, Hydrocharis, Butomus and Stratiotes are mined by the larvae of Hydrellia. Some of these plants float upon the water like duck-weed (Lemna).

Our knowledge of the life-histories of these species is brief. Apparently all the species of these two genera transform within their mines. Some produce linear mines while others make blotch mines.

Hydrellia

At least eleven leaf-mining species have been described from Europe. A North American species, *Hydrellia scapularis* described by Loew (1862) has been recorded as a leaf miner of Hordeum. In recent article De Ong (1922) states that the larvae of this species often causes severe damage to rice. He describes the habits of this species briefly. It

pupates in the leaves, emerging during the latter weeks of June. There is but one brood. The attacked leaves turn down and lay flat on the water. After a few weeks of warm weather the greater part of the affected plants sprout again.

Another species of Hydrellia was reared by Miss Moore (1915) from the leaves of *Potamogeton amplifolius* Pond weed. The larvae produced linear mines on the upper surface of the leaves. The puparium was formed at the ends of these mines.

Notiphila

The European species *N. flaveola* Meig., is a leaf miner on poppy and nasturtium. Goureau (1851) describes the mine of this species on nasturtium. It makes a blotch mine in the center of the leaf where the veins converge. The puparium is formed within the mine.

CORDYLURIDAE

Several European species belonging to the genus Parallelomma have been recorded as leaf-miners on wild lilies and orchids. In studying the North American leaf-mining species, Frost, frequently found a species of Diptera mining the leaves of Solomon's seal (Polygonatum) and the false Solomon's seal (Smilacina). Many larvae were reared and puparia secured but no adults emerged. Comparing these with the mines and puparia of the European species it was determined that the miner of Solomon's seal belonged to the genus Parallelomma.

The Solomon seal leaf-miner lays their pure white eggs in groups of two or three on the under surface of the leaf. The eggs are conspicuous against the green leaf and are about 1.5 to 2 mm. long. Even after the larvae have finished their mining the eggs shell can be found on the under surface of the leaf. The miners are gregarious several uniting their

efforts to produce a broad linear mine on the leaf, which is confined more or less between the larger parallel veins of the leaf. The entire contents of the leaf is eaten out including the parenchyma and the palisade cells leaving only the upper and lower epidermis. This being transparent gives the mine a whitish or pale green color. When mature the mine becomes marked about its edges with a conspicuous

FIG. 87. Mine of Parallelomma species? on Solomon's seal.

reddish margin. Little or no frass can be found within the mine. The puparia are formed outside the mine and the exit holes of the larvae are evident in the upper epidermis of the leaf.

FAMILY ANTHOMYIIDAE

The leaf-mining forms of calyptrate Diptera are included in the family Anthomyiidae. They are all moderately

large, and those known to be leaf-miners fall within three or four genera,—Pegomyia, Hylemyia, Chirosia, and perhaps Coenosia.

The two genera first named are well represented in North America and these will be discussed here.

The eggs. The eggs are linear—oblong, white and rather conspicuous for their size. They are laid singly or in small clusters, flatwise, on the under side of leaves, and on hatching the larvae enter the leaf immediately. The mine is at first linear but very soon it becomes blotched.

Fig. 88. Larva of Hylemyia fugax.

The larva. The larvae taper strongly to the front end and are blunt in the rear, with the last segment obliquely truncate and tuberculate above. The body segments are transversely wrinkled.

The adult. The flies have a wing expanse of less than half an inch. They are rather slender, grayish in color, and are rather thereby beset with stout black bristles. The legs are blackish in Hylemyia and yellowish in Pegomyia.

HYLEMYIA

Many of the species of Hylemyia mine in the roots, stems, and leaves of plants. To this genus belong several well-known species, such as the cabbage maggot (*Hylemyia brassicae*), the onion maggot (*H. antiqua*), and the seed-corn maggot (*H. cilicrura*). There are only a few known North American leaf-mining species in this genus.

The goose foot miner, *Hylemyia fugax,* is a fairly common miner on the leaves of spinach and beet and on the leaves of several weeds. In New York the species is not a serious pest on beets or spinach because of its relative scarcity and its preference for *Chenopodium album* as a host.

PEGOMYIA

Pegomyia is, for a large part, a mining genus. Some of the species mine in the roots of plants, and others in the stems;

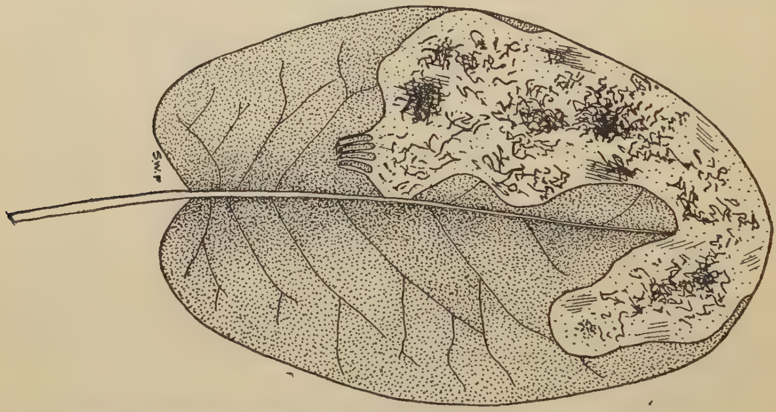

Fig. 89. Mine of Pegomyia calyptrata on dock, showing larvae

but the majority mine in the leaves. Fifteen authentic leaf-mining species have been recorded from various parts of the world. Only six of these are known to occur in America, the remainder being European species. Polygonaceae and Chenopodiaceae are the preferred hosts of this genus.

The characters by which the American leaf-mining species of Pegomyia can be separated in their egg and larva stages, have been presented by one of us (Frost '24), p. 99–100, in convenient tables.

FIG. 90. The beet leaf-miner, Pegomyia hyoscyami. *1*, adult ♂; *2*, mature larva; *3*, posterior spiracle; *4*, anterior spiracle; *5*, anterior end of larva, showing mouth hooks and sensory organs.

Two of the docks, *Rumex crispus* and *R. obtusifolius*, are extensively mined by several species of Pegomyia. Among these are two, *P. calyptrata* Zett, and *P. vanduzeei* Mall., which occur commonly throughout the United States. *P. calyptrata* is by far the commoner of the two species. The adult is readily distinguished by a bluish gray thorax and a reddish yellow abdomen. *P. vanduzeei*, on the other hand, is less common. It occurs about Ithaca, New York, abundantly in the early smmmer, but later in the season neither eggs, larvae, nor adults have been found. This species is distinguished by its inconspicuous gray color. The eggs of the dock miner are seldom laid singly, but are usually in groups of from three to five, or occasionally in groups of six or seven. They are normally placed in neat transverse rows on the under surface of the leaf.

The number of eggs occurring on a single leaf is surprising. As a rule one finds only five or six groups, but it is not uncommon to find more. In one instance twenty groups of eggs were found on a single leaf, 65 eggs in all; on another leaf, 16 inches long, eighteen groups containing 47 eggs. Not all the larvae from these eggs mature within the leaf on which they are laid, but some migrate and start new mines on other leaves.

The eggs hatch in from two to six days and the young larvae immediately enter the leaf, making small holes through the lower epidermis. All the eggs of a single group hatch at the same time and the larvae feed in a common mine, which is at first linear. The larvae mine side by side, progressing only in a forward direction. They keep close together, and all change their direction of mining at the same time, leaving behind them a short linear path. In about a day, although no definite time can be set, the larvae begin to enlarge their mine laterally, forming a blotch. They still remain in a common mine but separate in different

FIG. 91. A copy of DeGeer's figures of dipterous leaf-miners

directions. It is not an unusual sight to see several such blotches on a leaf. Each represents the work of a number of larvae that have hatched from a single group of eggs. These mines increase in size until they interfere with one another and a large blotch is produced covering the entire area of the leaf. Many of the larvae are naturally forced to abandon their mines and form new ones in other leaves. The presence of nearly mature larvae in small blotch mines is an indication that these larvae have entered fresh leaves.

The process of forming a new mine is as follows: At first the larva cuts a short slit in the epidermis of the leaf. Then, by inserting its mouth hooks in this slit and working them back and forth, it separates the lower and upper epidermal layers of the leaf. The larva then pushes the anterior end of its body into the small opening that it has made. After the first two segments have been forced through the opening, it is only a matter of a few minutes before the larva has worked its way completely within the leaf. This operation is accomplished with many vigorous twists of the body as it is drawn into the leaf. Larvae of the third instar bury themselves completely in the leaf in less than twenty minutes. The length of the larval period varies between 9 and 16 days. In warm weather the larvae mature rapidly, but in cooler weather they become inactive and the larval period may be prolonged for several days.

The mature larvae escape through the epidermis of the leaf but seldom make their exit through a definite hole. Usually the upper epidermis becomes dry and parchment-like, rupturing itself and allowing the larvae to escape. In some cases, however, the larvae cut circular holes through the epidermis. They fall to the ground and ordinarily penetrate the soil to a depth of 2 or 3 inches. Some of the puparia formed in June and July, as well as those formed in September, do not transform to adults in the same year that

they are formed, but overwinter as puparia and the adults issue in the following spring. This seems to be a provision of nature to insure the continuation of the race in the following year, in case all the indiviuals of any generation should perish.

CHAPTER XV

List of Leaf-Mining Insects[1]

(Compiled by S. W. Frost)

LEPIDOPTERA

Insect	*Host plants*
Eriocraniidae	
Eriocrania	
101 auricyanea Walsm.	89s, 90, 293s
Incurvariidae	
Paraclemensia	
102 acerifoliella Fitch	5
Nepticulidae	
Glaucolepis	
103 saccharella Braun	4, 6
Nepticula	
104 atella Braun	305
105 amelanchierella Clem.	26
106 anguinella Clem.	293s
107 apicialbella Cham.	390, 391, 392
108 argentifasciella Braun	380
badiocapitella Cham., see 161	
109 belfrageella Cham.	Unknown
110 bifasciella Clem.	284, 287
111 canadensis Braun	19
112 caryaefoliella Clem., see 128	
113 castaneaefoliella Cham.	89, 293s
114 ceanothi Braun	94
115 cerea Braun	Unknown
116 chalybeia Braun	292
ciliaefuscella Cham., see 125	
117 clemensella Cham.	268
118 condaliafoliella Busck	116
119 corylifoliella Clem.	63, 86, 121, 230

[1] Nos. 101 to 500 Lepidoptera, 501 to 600 Coleoptera, 601 to 700 Hymenoptera and 701 to 800 Diptera.

The letter "s" after the number of the host plant indicates that the insect mines in one or several of the species of the host genus.

For the name of the host plant see corresponding number in List of Host Plants of Leaf Mining Insects.

Insect		*Host plants*
120	crataegifoliella Clem.	123, 126, 127
	dallasiana F. & B., see 167	
121	diffasciae Braun	Unknown
122	discolorella Braun, see 125	
123	flavipedella Braun	295, 305
	furcotibiella Riley, see 125	
124	fuscocapitella Cham., see 156	
125	fuscotibiella Clem.	335
126	grandisella Cham.	Unknown
	hypericella Braun, see 464	
127	intermedia Braun	317s
128	juglandifoliella Clem.	176s, 178, 195, 196, 230
129	latisfasciella Cham.	89, 297, 307
	leucostigma Braun, see 107	
	maculosella Cham., see 133	
	marmaropa Braun, see 456	
	maximella Cham., see 141	
	minimella Cham., see 119	
132	myricafoliella Busck	220
133	nigriverticella Cham.	Unknown
134	nyssaefoliella Cham.	224
135	nyssæella Clem. (adult unknown)	223
136	obscurella Braun	219
137	opulifoliella Braun	228, 228½
138	ostryaefoliella Clem.	61, 62, 230
139	pallida Braun	335
140	paludicola Braun	232
141	platanella Clem.	268
142	platea Clem.	268, 293s
143	pomivorella Pack.	213, 284s
144	populetorum F. & B.	278
145	prunifoliella Clem.	284s
146	pteliaeella Cham.	290
147	punctulata Braun	93, 312
148	purpuratella Braun	Unknown
149	quadrinotata Braun	86, 121
	quercicastanella Cham., see 156	
150	quercipulchrella Cham.	293a, 294
151	resplendensella Cham.	Unknown
	rhamnella Braun, see 152	
152	rhamnicola Braun	313
153	rhoifoliella Braun	318, 319
154	rosaefoliella Clem.	324, 325
155	rubifoliella Clem.	326

Insect		*Host plants*
156	saginella Clem.	89s, 293s
157	scintillans Braun	124
	serotinaeella Cham., see 110	
158	similella Braun	305
159	slingerlandella Kearf.	284
	taeniola Braun, see 466	
160	terminella Braun	302, 305, 307, 308
161	thoracealbella Cham.	Unknown
162	tiliella Braun	380
163	trinotata Braun	176, 178
164	ulmella Braun	391, 392
165	unifasciella Cham.	293s
166	variella Braun	293
167	vilosella Clem.	326s, 328
	virginiella Clem., see 119	
167½	virgulae Braun	121
Tischeriidae		
Tischeria		
	admirablis Braun, see 467	
168	aënea F. & B.	326
169	ambrosiaeella Cham.	25
	albostraminea Walshm., see 170	
170	badiiella Cham.	293s
	castaneaeella Walshm., see 171	
171	castaneaeella Cham.	89s, 293s
	cinereotunicella Braun, see 466¼	
172	citripennella Clem.	158, 293s
	complanoides F. & B., see 184	
173	concolor Zeller	293s
174	fuscomarginella Cham.	293s
175	heliopsisella Cham.	25, 172
	latipenella Cham., see 184	
176	malifoliella Clem.	122s, 212, 213
	mediostriata Braun, see 466½	
	nolckeni F. & B., see 175	
177	nubila Braun	294
	omissa Braun, see 466¾	
178	pruinosella Cham., see 170	
180	quercitella Clem.	293s
	quercivorella Cham., see 180	
181	roseticola F. & B.	324s
182	solidaginisella Clem.	355s
183	tinctoriella Cham.	293s
184	zelleriella Clem.	293s

	Insect	*Host plants*
Lyonetiidae		
Proleucoptera		
185	albella Cham.	274s, 335s
186	smilaciella Busck	348s
Leucoptera		
	pachystimella Busck, see 468	
	robiniella Braun, see 469	
Lyonetia		
187	alniella Cham.	16s
	apicistrigella Cham., see 191	
188	candida Braun	314, 316
189	latistrigella Walk.	315
	nidificansella Pack., see 191	
189½	saliciella	337s
190	speculella Clem.	92½, 213, 406s
Phyllocnistis		
192	ampelopsiella Cham.	289
194	erechtitisella Cham.	149
	finitima Braun, see 467½	
	insignis F. & B., see 194	
195	intermediella Busck	345½
196	liquidambarisella Cham.	205
197	liriodendronella Clem.	206
198	magnatella Zell.	Unknown
199	magnoliella Cham.	211
200	populiella Cham.	274s
	smilacisella Cham., see 252	
201	vitifoliella Cham.	406s
202	vitigenella Clem.	406s
Bedellia		
203	sommulentella Zell.	193
Bucculatrix		
203½	Ainsliella Murt.	293s
204	ambrosiaeella Cham.	25
205	ambrosiaefoliella Cham.	23
	arnicella Braun, see 470	
205½	canadensisella Cham.	60
206	ceanothiella Braun	93s
206½	coronatella Clem.	63
207	crescentella Braun	47s, 150, 355
208	cuneigera Meyr.	52
	curvilineatella Pack., see 210	
	divisa Braun, see 471	
	errans Braun, see 208	

Insect		*Host plants*
209	eupatoriella Braun	152
209½	magnella Cham. (= niveela Cham.?)	294, 351s
	obscurofasciella Cham., see 211	
	packardella Cham., see 471	
210	pomifoliella Clem	213
	pomonella Pack., see 210	
	sexnotata Braun, see 471¾	
210½	thurberiella	164s, 379½
211	trifasciella Clem	89s
Gracilariidae		
Parornix		
	alata Braun, see 472	
	albifasciella Dietz, see 219.	
212	anglicella Stt	122s, 157s
213	crataegifoliella Clem	122
214	dubitella Dietz	Unknown
215	geminatella Pack	122s, 287, 291s
216	inusitatumella Cham	122s
217	palmiella Dietz	198½
218	prunivorella Cham., see 215	
219	quadripunctella Clem	26
220	spiraeifoliella Braun	370
Gracilaria		
	acerifoliella Cham., see 473	
	alnivoriella Cham., see 446	
220½	anthrobaphes Meyr	396
221	belfrageella Cham	118
221½	blandella Clem	178
222	burgessiella Zell	118
222½	cornusella Ely	118½
223	flavella Ely	220
224	ferrunginella Braun	316
225	glutinella Ely	16
226	hypericella Braun	185, 186
226½	invariabilis Braun	286½
227	juglandiella Cham	196
	juglandisigraella Cham, see 227	
228	juglandivorella Cham	196
	melanocarpae Braun., see 474	
229	negundella Cham	3
	plataginisella Cham., see 255	
230	porphyretica Braun	314s, 316
	purpuriella Cham., see 453	
231	rhoifoliella Cham	317, 319
	salicifoliella Cham., see 258	

	Insect	*Host plants*
232	sassafrasella Cham.	339
233	scutellariella Braun	342
233½	stigmatella Fab.	337s, 274s
234	superbifrontella Clem.	167
234½	syringella	375½
	thermopsella Cham., see 259	
234¾	umbratella Braun	6
235	violacella Clem.	216
Acrocercops		
236	affinis Braun	293s
237	albinotella Cham., see 237	
	arbutella Braun., see 475	
	duodecemlineella Cham., see 239	
	eupatoriella Cham., see 241	
238	onosmodiella Busck	226
	quercifoliella Cham., see 239	
239	strigifinitella Clem.	60, 89, 293s
240	strigosa Braun	306
241	venustella Clem.	154
Apohthisis		
244	pullata Braun	313
Leucanthiza		
245	amphicarpeaefoliella Clem.	156, 156½
246	dircella Braun	139
	saundersella Cham., see 245	
Marmara		
247	apocynella Braun	31, 32
247½	arbutiella Busck	36
248	auratella Braun	330
250	opuntiella Busck	229
251	salictella Clem.	335s
252	smilacisella Cham.	348, 349, 350
Parectopa		
	albicostella Braun, see 476	
253	astericola F. B.	47
	erigeronella Cham., see 256	
	geiella Cham., see 256	
254	lespedezaefoliella Clem.	204s, 216s
	mirabilis F. & B., see 254	
255	pennsylvaniella Engel	46
256	plantaginisella Cham.	150s
257	robiniella Clem.	216s, 321
258	salicifoliella Cham.	335s
259	thermopsella Cham.	378

Insect		*Host plants*
Cremastobombycia		
	actinomeridis F. & B., see 262	
260	ambrosiella Cham.	23, 25, 320
	bostonica F. & B., see 262	
	elephantopodella F. & B., see 262	
261	grindeliella Walsm.	166
	helianthisella Cham., see 262	
	helianthivorella Cham., see 262	
262	ignota F. & B.	141, 168, 170, 320, 399
263	solidaginis F. & B.	355
264	verbesinella Busck	399
Phyllonorycter, see Lithocolletis		
	felinella Heinrich., see 300½	
Lithocolletis		
266	aceriella Clem.	4, 5
	actinomeridis F. & B., see 262	
	aenigmatella F. & B., see 317	
267	aeriferella Clem.	300
	aesculella Riley, see 268	
268	aesculisella Cham.	9½, 10
269	affinis F. & B.	207s, 373s
270	agrifoliella Braun	293
271	albanotella Cham.	295, 301, 304
272	alni Walshm.	16s
273	alnicolella Walshm.	17
274	alnifoliella Hubn.	16s
	alnivorella Cham., see 272	
	alternatella Zell., see 308	
	alternata Cham., see 308	
275	ambrosiaeella, see 260	
	amoena F. & B., see 260	
	amorphae F. & B., see 356	
	amorphaeella Cham., see 356	
	amphicarpaeella Cham., see 326	
276	apicinigrella Braun	335s
277	arbutusella Braun	36
	arculella Braun	unknown
278	argentifimbriella Clem.	293s
279	argentinotella Clem.	390, 391
	arizonella Braun, see 479	
	atomariella Zell., see 346	
280	auronitens F. & B.	18
281	basistrigella Clem.	293s

	Insect	*Host plants*
282	bethunella Cham.	393s
283	betulivora Walsh.	63
	bicorella Cham., see 293	
	bifasciella Cham., see 329	
284	blancardella Fabr.	122s, 284s, 293s
	bolliella Dyar., see 349	
	bostonica F. & B., see 262	
285	caryaealbella Cham.	178
	caryalbella Walsh., see 285	
286	caryaefoliella Clem.	178, 195, 196
287	castaneaeella Cham.	89, 293s
	castanella Walsh., see 287	
288	celtifoliella Cham.	96
289	celtisella Cham.	96
	ceriferae Walshm., see 329	
290	cervina Walshm.	Unknown
291	cincinnatiella Cham.	294
292	clemensella Cham.	5
293	conglomeratella Zell.	295, 309
	consimilella F. & B., see 354	
	coryliella Cham., see 294	
294	corylisella Cham.	121
295	crataegella Cham.	122s, 127, 284, 287, 291s
	cretaceella Braun, see 480	
295½	deceptusella Cham.	122s
296	desmodiella Clem.	204, 217, 251
297	diaphanella F. & B.	295, 299
298	diversella Braun.	160, 233
299	eppelsheimi F. & B. (N. A. ?)	176s
300	fasciella Walshm.	293s
300½	felinella Heinrich.	269
301	fitchella Clem.	293s, 295, 301
302	fletcherella Braun.	294
303	fragilella F. & B.	207
	fuscocostella Cham., see 278	
304	gaultheriella Walshm.	159
305	gemmea F. & B.	323
	gregariella Murt., see 296	
306	guttifinitella Clem.	319
307	hageni F. & B.	295, 296, 306
308	hamadryadella Clem.	211s, 230, 294
	hamadryella Dyar, see 308	

Insect		*Host plants*
309	hamameliella Busck........................	167
	hamamelis Smith ?, see 309	
	ignota F. & B., see 262	
310	incanella Walshm............................	17
311	insignis Walshm.............................	95
	intermedia F. & B., see 281	
	inusitatella Braun, see 481	
	juglandiella Clem., see 286	
312	kearfottella Braun..........................	89
	lebertella F. & B., see 282	
314	ledella Walshm..............................	202
315	lentella Braun..............................	63, 230
316	leucothorax Walsm..........................	298
	longistriata F. & B., see 278	
	longirostrata Dyar, see 278	
317	lucetiella Clem..............................	380
318	lucidicostella Clem..........................	5
	ludicostella Riley, see 318	
319	lysimachiaeella Cham........................	371
320	macrocarpella F. & B........................	301
321	malimalifoliella Braun......................	124, 128, 213
	manzanita Braun, see 428	
322	mariaeella Cham.............................	374
323	martiella Braun.............................	63
324	mediodorsella Braun.........................	293s
325	minutella F. & B............................	307
	mirifica F. & B., see 335	
	modesta F. & B., see 358	
326	morrisella Fitch............................	156
	necospinusella Cham., see 307	
327	nemoris Walshm..............................	396
	nonfasciella Cham., see 289	
328	obscuricostella Clem........................	230
329	obstrictella Clem...........................	294, 303, 307
	obtusilobae F. & B., see 293	
330	occitanica F. & B...........................	389s
331	olivaeformis Braun..........................	177
332	oregonensis Walshm..........................	373
	ornatella Cham., see 333	
333	ostensackenella Fitch.......................	321, 323
334	ostryarella Cham............................	86, 230
335	ostryaefoliella Clem........................	230, 293s.
	pernivalis Braun, see 477	
336	picturatella Braun..........................	219

Insect		Host plants
337	platanoideiella Braun	294, 295, 301
338	populiella Cham.	274
339	propinquinella Braun.	287
	pseudacaciella Fitch, see 343	
	pusillifoliella F. & B., see 289	
340	quercialbella Fitch.	293s
	quercibella Cham., see 340	
	quercifoliella Fitch, see 301	
	quercipulchella Cham., see 340	
	quercipulchrella Riley, see 340	
	quercitorum F. & B., see 301	
341	quercivorella Cham.	307
342	rileyella Cham.	293s
343	robiniella Clem.	321, 323
344	roboris Zett.	293s
345	saccharella Braun	6, 7
346	salicifoliella Clem	276, 335s
347	salicivorella Braun	335s
348	scudderella F. & B.	335s
	solidaginis F. & B., see 263	
	solidaginisella Cham., see 263	
	subaureola F. & B., see 271	
	superimposita Braun, see 478	
349	symphoricarpella Cham.	374
	symphoricarpella F. & B., see 349	
	tenuistrigata F. & B., see 342	
	texanella Zell., see 326	
350	tiliacella Cham.	380
	tiliaeella Cham., see 350	
	tiliella Walshm., see 350	
	toxicodendri F. & B., see 306	
351	tremuloideella Braun.	280
352	trifasciella (?Haw) F. & B.	207, 374
353	trinotella Braun.	5
354	tritaenianella Cham.	230
	tritaeniella Dyar, see 354	
355	tubiferella Clem.	294
356	uhlerella Fitch.	27
357	umbellulariae Walshm.	393
358	ulmella Cham.	390, 391
	unifasciella Cham., see 300	
	verbesinella Busck, see 264	
359	viburnella Braun.	400
	virginiella Cham., see 328	

	Insect	*Host plants*
	Coleophoridae	
	Coleophora	
	annulicola Braun, see 483	
360	cretaticostella Clem.	273, 326s
361	fletcherella Fern.	122s, 213
362	granifera Braun	52
363	laricella Hubn.	200
	occidentis Zell., see 265	
364	ostryae Clem.	230, 293s
	piperata Braun, see 484	
365	pruniella Clem.	287
366	querciella Clem.	293s
367	quercifoliella Clem.	293s
368	tiliaefoliella Clem.	380
369	viburnella Clem.	401
370	volckei Heinrich	213
	Elachistidae see Cycnodiidae	
	Cycnodiidae	
	Elachista see Aphelosetia	
	Aphelosetia	
371	albicapitella Engel	272
	albipalpella Clem., see 381	
372	argentosa Braun	82s
373	brachyelytrifoliella Clem.	69
	cristatella Cham., see 381	
374	cucullata Braun	84
375	enitescens Braun	340
375½	inaudita Braun	340s
376	irrorata Braun	13, 234
377	leucofrons Braun	143s, 187s
378	madarella Clem.	82, 83, 340
379	orestella Busck	187
380	praelineata Braun	187
381	prematurella Clem.	14, 143s, 187s, 271
382	radiantella Braun	235s
	salinaris Braun, see 485	
383	solitaria Braun	235s
384	sylvestris Braun	272
	Homaledra see Lavernidae	
	Heliozelidae	
	Antispila	
384¼	ampelopsifoliella Cham.	289, 406s
384¾	argentifera Braun	60?

Insect		*Host plants*
385	aurirubra Braun	118s, 120½
386	cornifoliella Clem	119, 120
387	hydrangiaeella Cham	184
388	isabella Clem	406s
389	nyssaefoliella Clem	223, 224
390	viticordifoliella Clem	406
390½	voraginella Braun	405½
Coptodisca		
	cercocarpella Braun, see 486	
391	diospyriella Cham	138
392	juglandiella Cham	196
392½	Kalmiella Dietz	198½
393	lucifluella Clem	178
394	magnella Braun	160
395	negligens Braun	232
396	ostryaefoliella Clem	230
	pruniella Clem., see 400	
397	quercicolella Braun	293s
	ribesella Braun, see 487	
398	saccatella Pack, see 400	
399	saliciella Cham	335
400	splendoriferella Clem	122s, 128, 213, 274s, 287, 291
Gelichiidae		
Gelechia		
401	petasites Pfaff. (N. A. ?),	247
	physaliella Cham., see 408	
402	pseudoacaciella Cham	Invading mines
	scutellariaella Cham., see 407½	
	smiliella Cham., see 405	
	solanieella Cham., see 405	
Gnorimoschema		
403	artemisiella Kearf	355
404	erigeronella Braun	150
Phthorimaea		
	cinerella Murt., see 405	
405	glochinella Zell	351, 353
	inconspicuella Murt., see 405	
406	operculella Zell	222, 354
407	polemoniella Braun, see 489	
	sacculicola Braun, see 488	
	solanella Bdv., see 406	
	solaniella Cham., see 405	

Insect		*Host plants*
$407\frac{1}{2}$	scutellariaella Cham.	$342\frac{1}{2}$
	tabacella Rag., see 406	
Paralechia		
408	pinifoliella Cham.	261
Aristotelia		
409	physaliella Cham.	255
	bellela Walk., see 411	
410	robusta Braun	340
411	roseosuffusella Clem.	382
Chrysopora		
	armeniella F. & B., see 412	
	hermannella Cham., see 412	
412	lingulacella Clem.	54s, 99s
$412\frac{1}{2}$	hermannella Fabr.	54s, 99s
Recurvaria		
	abietisella Pack, see 413	
413	apicitripunctella Clem.	$388\frac{1}{2}$, 257
414	ceanothiella Braun	94
415	juniperella Kearf.	197
416	milleri Busck	259
417	moreonella Heinrich	262
418	nanella Hubn.	122s, 213, 284s, 291s
	nigra Kearf., see 420	
419	obliquistrigella Cham.	198
420	piceaella Kearf.	256
$420\frac{1}{2}$	piceaella nigra Kearf.	256
421	pinella Busck	260
422	thujaella Kearf.	379
Evippe		
423	prunifoliella Chem.	3s, 284s
Nealyda		
424	bifidella Dietz	15
425	kinzelella Busck	263
426	pisoniae Busck	264
Tosca		
427	plutonella Heinrich	284s
Lavernidae		
Homaledra		
$427\frac{1}{2}$	sabalella Cham.	421, 422
Psacaphora		
428	argentimaculella Murt.	412
	communis Braun, see 490	
	engelella Busck, see 433	

	Insect	*Host plants*
430	cephalanthiella Cham.	97
431	metallifera Walshm.	244
432	sexstrigella Braun	146
433	terminella Westw.	110
	Cosmopteryx	
434	clandestinella Busck	236
435	clemensella Stainton	85
436	gemmiferella Clem.	192s, 239
437	opulenta Braun	24
438	pulchrimella Cham.	258
	Chrysopeleia	
440	ostryaella Cham.	230
441	purpuriella Cham.	307
	Yponomeutidae	
	Yponomeuta	
442	padella Linn.	122s, 284s, 406s
	Argyresthia	
443	annettella Busck	197
444	austerella Zell.	293s
445	thuiella Pack.	379
	Scythris	
446	alnivorella Cham.	16s
447	alnivorella alnicolella Cham.	16s
	brevistriga Cham., see 451	
	buristriga Cham., see 451	
	dorsipallidella Cham., see 451	
450	graminivorella Braun	187, 270
	immaculatella Cham., see 451	
451	impositella Zell.	45s
452	matutella Clem., see 451	
	monstratella Walk., see 451	
453	purpuriella Cham.	274s
	Glyphipterygidae	
	Choreutis	
455	gnaphaliella Kearf.	29s, 163s
	Heliodinidae	
	Cycloplasis	
456	panicifoliella Clem.	236
	Lithariapteryx	
457	abroniaeella Cham.	1

Insect		Host plants
Tortricidae		
Epinotia		
458	heucherana Heinrich	174
459	nanana Treit	256
460	ruidosana Heinrich	175
Polychrosis		
463	magnoliana Kearf	211s
Pyralidae see 494		
Noctuidae see 492		
Additional species[2]		
Nepticula		
464	hypericella Braun	185½
465	marmaropa Braun	325½
466	taeniola Braun	25½
Tischeria		
466¼	cinereotunicella Braun	295, 300
466½	mediostriata Braun	298¼
466¾	omissa Braun	20
467	admirabilis Braun	412
Phyllocnistis		
467½	finitima Braun	344s
Leucoptera		
468	pachystimella Busck	233½
469	robinella Braun	322
Bucculatrix		
470	arnicella Braun	40
471	divisa Braun	56½
471½	packardella Cham	89s, 155s, 293s
471¾	sexnotata	47
Ornix		
472	alata Braun	25½
Gracilaria		
437	acerifoliella Cham	2½
474	melanocarpae Braun	285½
Acrocercops		
475	arbutella Braun	35½
Parectopa		
476	albicostella Braun	401½
Lithocolletis		
477	pernivalis Braun	2½
478	superimposita Braun	2½
479	arizonella Braun	35½

[2] Made necessary chiefly because of newly described species.

Insect		*Host plants*
480	cretaceella Braun	298½
481	inusitatella Braun	293
482	manzanita Braun	36½
Coleophora		
483	annulicola Braun	45s, 355s.
484	piperata Braun	61, 335s.
Elachista		
485	salinaris Braun	241½
Coptodisca		
486	cercocarpella Braun	411
487	ribesella Braun	319½
Phthorimaea		
488	sacculicola Braun	355s
489	polemoniella Braun	273
Psacaphora		
490	communis Braun.	146
Microcalyptris		
491	scirpi Braun	341½
Noctuidae		
Arzama		
492	obliqua Walk	413
Nonagria		
493	oblonga Grote	413
Pyralidae		
Autocosmia		
494	helianthales Murt	171s
Melitara		
495	prodenialis Wlk	229

COLEOPTERA

Buprestidae		
Brachys		
501	aerosa Melsh	176s, 274s, 293s, 390, 380s
502	aeruginosus Gory	155
503	ovatus (Web.)	274s, 293s
	terminans C. & G., see 503	
	tessellatus Melsh., see 501	
Pachyscheius		
504	laevigatus (Say.)	203, 216, 217 418
	ovatus Say., see 504	
505	schwarzi Kerr	Unknown

Insect		Host plants
Taphrocerus		
506	gracilis (Say.)	341
Chrysomelidae		
Zeugophora		
507	abnormis (Lec.)	274s
508	consanguinea Crotch	Unknown
509	puberula Crotch	Unknown
510	scutellaris Suffr.	274s
511	varians Crotch	Unknown
Monoxia		
	consputa (Lec.), see 536	
Phyllotreta		
511½	aenicollis (Crotch)	203
512	chalybeipennis (Cr.)	77
513	liebecki Schaeffer	203
	sinuata Steph., see 514	
514	zimmermanni (Crotch.)	203
Hippuriphila		
515	modeeri (Linn.)	333, 334
Epitrix, see 537		
Mantura		
	floridana Cr., see 538	
Dibolia		
	aerea Melsh., see 516	
516	borealis Chev.	267
Microrhopala		
517	floridana Schwarz	108
517½	rubrolineata var. vulnerata Horn	358
518	vittata (Fab.)	359, 362, 364
519	xerene (Newm.)	68, 345, 357, 359, 361
Uroplata		
520	porcata (Melsh.)	235
Stenopodius		
520½	flavidus Horn	368½
Octotoma		
521	marginicollis Horn	246½
522	plicatula (Fab.)	67, 204s
Anoplitis		
523	inaequalis	47, 50, 51, 88, 118s, 151s, 154, 213, 322, 323, 394
	nervosa (Panz), see 523	
	suturalis, see 523	
524	rosea (Web.)	213

	Insect	*Host plants*
	Chalepus	
525	ater Weise	252s
526	bicolor (Oliv)	240
527	dorsalis Thunb.	27, 60s, 122, 155, 294, 307, 323
528	horni (Smith)	$121\frac{1}{2}$, 156
529	notatus (Oliv.)	$376\frac{1}{2}$
	nervosa Panz, see 523	
530	scapularis (Oliv.)	162
	scutellaris Oliv., see 527	
	omoger (Chap.), see 525	
	Baliosus	
531	californicus (Horn)	95
532	ruber (Weber)	3s, 26, 41, 60s, 112, 121s, 213, 284s, 288, 293s, 323, 380
	Hispa	
	rosea Weber, see 524	
	suturalis Fab., see 523	
	Curculionidae	
	Orchestes	
	minutus Horn, see 535	
534	pallicornis Say	213, 291s, 389, 390
535	rufipes Lec.	61, 275, 336, 337, 414, 415, 416
	Prionomeris	
$535\frac{1}{2}$	calceatus (Say.)	206, 339s
	Chrysomelidae	
	Monoxia	
536	consputa (Lec.)	166s
	Epitrix	
537	cucumeris Har.	351s
	Mantura	
538	floridana Cr.	417

HYMENOPTERA

	Tenthredinidae	
	Metallus	
	bethunei Mac. G., see 605	
603	capitalis Norton	326s
604	rhoweri Mac. G.	326s
605	rubi Forbes	326s

Insect	*Host plants*
Scolioneura	
606 populi Marl.	279
Fenusa	
607 curta Norton	301
608 dohrni Tischb.	16
melanopoda Cam., see 608	
nigricans Thoms, see 608	
pumila Brischke, see 608	
Kaliofenusa	
fulginosa Healy, see 698½	
intercus Fall., see 607½	
intermedia, see 609	
minima Brischke, see 608½	
608½ pumila Kl.	64
pusilla Lep., see 608½	
pygmaea Zett., see 608½	
tantilla Costa., see 608½	
609 ulmi Sund.	390
Profenusa	
610 *collaris* Mac. G.	127, 285
Phlebatrophia	
611 mathesoni Mac. G.	60s
612 nemorata Fall.	60
parviceps Newm., see 612	
tenella Zadd., see 612	
Schizocerus	
613 tristis fumipennis Dyar	8
614 prunivorus Marl.	284s
615 zabriskei Ashm.	281

DIPTERA

Cecidomyiidae	
Monarthropalpus	
701 buxi Lab.	76
Trypetidae	
Acidia	
703 heraclei Linn.	136, 173, 246, 283
Agromyzidae	
Agromyza	
704 allecta Melander	37, 65, 153
705 angulata Loew	131, 187, 254, 97½
706 borealis Mall.	190, 191

Insect		*Host plants*
707	clara Mel	92
708	coniceps Mall	367
709	coquilletti Mal	56, 143, 180, 385, 386, 409
710	curvipalpis var. texana Mall	23, 45, 47, 50, 51, 53, 154, 221, 356, 357, 359, 360, 361, 365, 366, 310
711	eupatoriae Mall	151
712	felti Mall	79, 80
713	fragariae Mall	157, 326s, 327, 329
714	inaequalis Mall	250, 402
715	inconspicua Mall	12
716	laterella Zett	194
717	maculosa Mall	37, 38, 45s, 66, 102, 108, 407
718	marginalis Mall	245
719	maura var. nasuta Mel	202½
720	melampyga Loew	267, 253
721	neptis Loew	409
722	parvicornis Loew	140, 237, 241, 242, 250, 386, 409
723	platyptera var. coronata Loew	50 357 359, 360, 397, 405
724	platyptera var. jucunda V. d. W	2, 20, 23, 31, 48, 129, 130, 150s, 168, 173, 192, 214, 224½, 252, 331, 355, 358, 359, 361, 397, 408, 410
725	posticata Meig	45, 49, 50, 51, 53, 205, 206½, 210, 215, 289, 354, 356, 357, 359, 360, 361, 363

Insect		*Host plants*
726	pusilla Meig.	22, 42, 43, 44, 35, 58, 71, 72, 74, 78, 81, 109, 113, 164, 182, 153, 154, 199, 201, 215 218, 214, 265, 266s, 311, 343, 346, 368, 369, 381, 382, 383, 384, 388, 354, 404, 409
727	reptans var. subnigripes Mall.	23, 25, 168, 394, 395
728	scutellata Fall.	81½, 100, 134, 168, 205, 206½, 215, 289, 407, 409
729	ulmi Frost.	390
730	viridula Coq.	307
	youngi, see 719	
731	species near luctuosa	131
732	species near pruinosa	183
733	species	277, 341
Cerodonta		
734	femoralis Meig.	56, 75, 98, 140, 133, 142, 144, 148, 179, 181, 182, 235, 238, 241, 242, 249, 254, 271, 215, 343, 375, 386, 403, 409
Napomyza		
735	lateralis Fall.	101s
Phytomyza		
736	affinis Fall.	70, 74, 246
737	albiceps Meig.	50, 51, 53, 173, 246, 265, 267, 363, 373

Insect		*Host plants*
737½	angelicella Frost	28½
738	aquifolii Gour?	188
739	aquilegiae Hardy (in Am. literature)	33, 34, 388
740	chrysanthemi Kowarz	23, 29, 65, 72, 101, 102, 103, 104, 105, 106, 107, 135, 151s, 168, 169, 171, 208½, 246, 265, 267, 344, 363, 376
	clematidis Loew, see 743½	
742	ilicis Curtis	188, 189
743	lactuca Frost	199
743½	loewii Hendel	114
744	nitida Mel	23, 221, 376, 377
745	obscurella Fall	9, 103, 208, 209, 338
746	obscurella var. nigritella Zett	28, 137, 287
747	palliata Coq., see 750½	
748	plantaginis R-D	266, 267
749	plumiseta Frost	33, 377
750	solidaginis R-D	266, 267
Antineura		
750½	palliata Coq	281s
Scaptomyza		
751	adusta Loew	21, 39, 70, 72, 74, 78, 265, 311
752	flaveola Meig	70, 72, 73, 74, 115, 243, 265, 311, 351, 372, 387
753	graminum Fall	34, 70, 72, 74, 248
Hydrellia		
754	scapularis Loew	180s
755	new species	282
Anthomyiidae		
Hylemyia		
760	betarum Lintn	58
761	floccosa Macq	58, 73
762	fugax Meig	21, 58, 99, 369
763	substriata Stein	58, 59,

Insect		*Host plants*
Pegomyia		
764	bicolor Wied.	333, 334
765	calyptrata Zett.	333, 334
766	hyoscyami Panz.	21, 54, 55, 57, 58, 99, 225, 369
767	ruficeps Stein.	58
768	vanduzeei Mall.	333, 334
769	winthemi Meig.	333, 334
770	species	332

CHAPTER XVI

Host Plants of Leaf-Mining Insects

(Compiled by S. W. Frost)

	Host	*Insects*[1]
1	Abronia fragrans Nutt	457
2.	Abutilon abutilon (L.) Rusby	724
2½.	Acer grandidentatum	473, 477, 478
3.	Acer negundo L.	229
	Acer nigrum Michx., see 7	
4.	Acer rubrum L.	103, 266
5.	Acer saccharinum L.	102, 266, 292, 318, 353, 461
6.	Acer saccharum Marsh.	103, 345, 234¾
7.	Acer saccharum var. nigrum Michx.	345
	Acer species	423, 501, 532
8.	Acmispon grandiflora	613
9.	Actaea rubra (Ait.) Willd.	745
	Actinomeris alternifolia (L.), see 320	
	Actinomeris aquarrosa Nutt., see 320	
	Aesculus flava Ait., see 11	
10.	Aesculus glabra Widenow	268
11.	Aesculus octandra Marsh.	268
12.	Agropyron species	715
13.	Agrostis perennans (Walt) Tuckerm.	376
14.	Agrostis species	381
	Ague tree, see 339	
	Alder, see 16	
	Alfalfa, see 215	
15.	Allionia nyctaginea (Michx.)	424
16.	Alnus alnus (L.) Britton	225, 608
	Alnus glutinosa, see 16.	
17.	Alnus incana (L.) Medic.	273, 310
18.	Alnus rubra (Marsh) Desf.	280
	Alnus serrulata Willd, see 18	

[1] Nos. 1 to 500, Lepidoptera; Nos 501 to 600, Coleoptera; Nos. 601 to 700, Hymenoptera, and Nos. 701 to 800, Diptera. For the name of the insect see corresponding numbers in List of Leaf-mining Insects. For Synonymy of Botanical Names, H. O. House, N. Y. State Museum Bull. 254, 1924, has been followed.

	Host	*Insects*
19.	Alnus tenuifolia ?	111
	Alnus vulgaris Hill, see 16	
	Alnus species	187, 272, 274, 446, 447
20.	Althea rosea Cav.	724, $466\frac{3}{4}$
	Alum root, see 174	
21.	Amaranthus retroflexus L.	62, 751, 766
22.	Amaranthus viridis L.	726
	Ambrosia artemisiifolia (L.), see 23	
23.	Ambrosia elatior var. artemisiifolia (L.) House	205, 260, 710, 724, 727, 740, 744
24.	Ambrosia psilostachya D. C.	437
25.	Ambrosia trifida L.	169, 175, 204, 260, 275, 727
$25\frac{1}{2}$	Amelanchier alnifolia	466, 472
26.	Amelanchier canadensis (L.) Medic.	105, 219, 532
	American aspen, see 280	
	American elm, see 390	
27.	Amorpha fruticosa L.	356, 527
	Ampelopsis quinquefolia Michx., see 289	
	Amphicarpa moenica (L.) Eil., see 156	
28.	Amygdalus persica L.	746
	Andropogon sorghum Brot., see 179	
$28\frac{1}{2}$	Angelica atropurpurea	736s, $737\frac{1}{2}$
	Annual sow thistle, see 368	
29.	Antennaria plantaginifolia (L.) Richards	740
	Antennaria species	455
30.	Anthyllis vulneraria L.	752
	Apios tuberosa Moench., see 162	
31.	Aplopappus squamosa ?	724
32.	Apocynum cannabinum L.	247
	Apple, see 213	
33.	Aquilegia canadensis L.	739, 749
34.	Aquilegia vulgaris L.	739, 753
35.	Arabis laevigata (Muhl.) Poir	726
	Arborvitae, see 379	
$35\frac{1}{2}$	Arbutus arizonica	475, 479
36.	Arbutus menziesii	277, $247\frac{1}{2}$
	Arcotostaphylos manzanita	482
37.	Arctium lappa L.	704, 717
38.	Arctium minus (Hill) Bernh.	717
39.	Armoracia armoracia (L.) Cockerell	751
40.	Arnica cordifolia	470

	Host	*Insects*
41.	Aronia arbutifolia L.	532
	Arrow-wood, see 400	
42.	Asclepias incarnata L.	726
43.	Asclepias syriaca L.	726
44.	Asclepias tuberosa L.	726
	Ash, see 158	
	Aspen, see 274	
	Asplenium pinnatifidum Nutt., see 79	
	Aster, see 45 and 345	
45.	Aster arvensis	710, 725
46.	Aster cordifolius L.	255
	Aster corymbosus Ait., see 47	
47.	Aster divaricatus L.	253, 523, 710
48.	Aster ericoides L.	724
49.	Aster laevis L.	725
	Aster-like boltonia, see 68	
50.	Aster novae-angliae L.	523, 710, 723, 735, 737
51.	Aster paniculatus Lam.	523, 710, 725, 737
52.	Aster shortii Lindl.	208, 362
53.	Aster undulatus L.	710, 725, 737
	Aster species	207, 451, 483, 717
54.	Atriplex hortensis L.	766
55.	Atriplex Patula L.	766
	Atriplex species	412
56.	Avena sativa L.	709, 734
	Azalia, see 316	
56½	Balsamorrhiza sagittata	471
	Balsam poplar, see 276	
	Baneberry, see 9	
	Barbarea vulgaris, see 78	
	Barley, see 182	
	Barnyard grass, see 140	
	Basswood, see 380	
	Bayberry, see 219	
	Bay-leaved willow, see 337	
	Bean, see 162, 250, 252	
	Bearded short husk, see 69	
	Beard grass, see 179	
	Beech, see 155	
	Beet, see 59	
	Beggarticks, see 65	
	Bent grass, see 13	

	Host	*Insects*
57.	Beta cicla	766
58.	Beta vulgaris	726, 760, 761, 762, 763, 766, 767
59.	Beta vulgaris macorhiza	763
60.	Betula alba L.	$205\frac{1}{2}$, 612
61.	Betula frontalis	138, 484
62.	Betula glandulosa Michx.	138
63.	Betula lenta L.	119, $206\frac{1}{2}$, 283, 315, 323
64.	Betula populifolia Marsh.	$608\frac{1}{2}$
	Betula species	239, $384\frac{3}{4}$, 527, 532, 611, 612
65.	Bidens frondosa L.	704, 740
66.	Bidens leucantha	717
67.	Bigonia radicans L.	522
	Birch, see 60	
	Bitternut, see 176	
	Bittersweet, see 352	
	Blackberry, see 326	
	Black-cap raspberry, see 326	
	Black Jack oak, see 302	
	Black walnut, see 196	
	Blue bell, see 273	
	Blue flag, see 194	
	Blue grass, see 270	
	Blue sailor, see 109	
68.	Boltonia asteroides (L.) L'Her.	519
	Boneset, see 151	
	Bottle brush grass, see 187	
	Box elder, see 3	
	Boxwood, see 76	
69.	Brachyelytrum erectum (Schreb.) Beauv.	373
70.	Brassica campestris L.	736, 751, 752, 753
71.	Brassica napus L.	726
72.	Brassica oleracea L.	726, 740, 751, 752, 753
73.	Brassica oleracea var. botrytis	752, 761
74.	Brassica rapa L.	726, 736, 751, 752, 753
	Brier, see 348	
	Broad-leaved-dock, see 334	

	Host	*Insects*
92.	Catalpa bungei	707
	Cat brier, see 348	
	Catmint, see 221	
	Catnep, see 221	
	Cat tail, see 413	
92½.	Ceanothus americanus	190
93.	Ceanothus cuneatus	147
94.	Ceanothus divaricatus Nutt.	114
94½.	Ceanothus fendleri Gray	531
95.	Ceanothus integerrimus H. & A.	311, 531
	Ceanothus species	206
96.	Celtis occidentalis Linn.	288, 289
97.	Ceplahalthus occidentalis L.	430
	Cerasus serotina, see 287	
	Cercocarpus ledifolius, see 411	
97½.	Chaetochloa glauca	705
98.	Chaetochloa viridis (L.)	734
	Chamaenerion angustifolium, see 146	
	Checkerberry, see 159	
	Cheeses, see 214	
99.	Chenopodium album L.	762, 766
100.	Chenopodium botrys L.	728
	Chenopodium species	412
	Cherry, see 255, 284	
	Chestnut, see 89	
	Chicory, see 109	
	Chinquapin, see 90	
101.	Chrysanthemum frutescens	740
102.	Chrysanthemum indicum	717, 740
103.	Chrysanthemum leucanthemum L.	740, 745
104.	Chrysanthemum morifolium	740
105.	Chrysanthemum parthenifolium	740
106.	Chrysanthemum parthenium (L.) Bernh.	740
107.	Chrysanthemum sinense	740
	Chrysanthemum species	735
108.	Chrysopsis graminifolia (Michx)	517
109.	Cichorium intybus L.	726
110.	Circaea alpina L.	433
	Circaea lutetiana L., see 110	
111.	Cirsium spinossiumus Walt.	728
112.	Citrus aurantium	532
113.	Citrullus vulgaris Schrad.	726
114.	Clematis species	741
	Clotbur, see 407	
	Clover, see 204, 218, 381	

	Host	*Insects*
128.	Cydonia species	321, 400
129.	Cynara scolymus	724
130.	Cynoglossum officinale L.	724
131.	Cyperus acuminatus T. & H.	705, 731
132.	Cyrtandra paludosa	700 (Hawaii)
133.	Dactylis glomerata L.	734
134.	Dahlia variabilis	728
	Daisy, see 101	
	Dandelion, see 202½	
135.	Daucus carota L.	740
136.	Deringa canadensis (L.) Kuntz	703
	Desmodium dillemii Darlington, see 216	
	Desmodium viridiflorum (L.) Kuntze, see 217	
137.	Diervilla diervilla (L.) MacM.	746
	Diervilla lonicera, see 137	
138.	Diospyros virginiana L.	391
139.	Dirca palustris L.	246
	Dock, see 248, 332	
	Dogwood, see 118	
140.	Echinochloa crus-galli (L.) Beuav.	722, 734
	Egg plant, see 353	
141.	Elephantopus carolinianus Willd.	262
	Elephant's foot, see 141	
142.	Eleusine indica (L.) Gaertn.	734
	Elm, see 389	
143.	Elymus canadensis L.	709
144.	Elymus glaucus Buckley	734
145.	Elymus species	377, 381
146.	Epilobium angustifolium L.	432, 490
148.	Eragrostis species	734
149.	Erechtites hieracifolia (L.) Raf.	194
150.	Erigeron speciosus D. C.	404
	Erigeron species	207, 256, 724
	Eupatorium ageratoides L., see 154	
151.	Eupatorium odoratum	711
152.	Eupatorium perfoliatum L.	209
153.	Eupatorium purpureum L.	704, 726
154.	Eupatorium urticaefolium Richard	241, 523, 710, 726
	Eupatorium species	740
	Everlasting, see 29, 163	
155.	Fagus species	471½, 502, 527
156.	Falcata comosa (L.) Kuntz	245, 528

	Host	*Insects*
171.	Helianthus multiflorus ?	740
	Helianthus species	262, 275, 494
172.	Heliopsis species	175
	Hemp, see 31	
173.	Heracleum lanatum Michx	703, 724, 737
174.	Heuchera americana L.	458
175.	Heuchera wootoni	460
	Hickory, see 176	
176.	Hicoria cordiformis (Wang) Britton	163
177.	Hicoria illinoensis (Wang) K. Koch	331
	Hicoria minima Marsh, see 176	
178.	Hicoria ovata (Mill) Britton	128, 163, 221½, 285, 286, 393
	Hicoria species	299, 501
	Hog peanut, see 156	
	Hog weed, see 23	
179.	Holcus sorghum L.	734
	Holly, see 188	
	Holly hock, see 20	
	Honeysuckle, see 137, 207	
	Honeywort, see 136	
	Hop hornbeam, see 230	
	Hops, see 183	
	Hop tree, see 290	
180.	Hordeum jubatum L.	709
181.	Hordeum murinum L.	734
182.	Hordeum vulgare L.	726, 734
	Hordeum species	754
	Hornbeam, see 87	
	Horse nettle, see 351	
	Horse radish, see 40	
	Hosackia grandiflora, see 8	
	Hound's tongue, see 130	
	Huckleberry, see 396	
183.	Humulus lupulus L.	732
	Hydrangea, see 184	
184.	Hydrangea cinerea Small	387
185.	Hypericum cistifolium Lam	226
185½.	Hypericum prolificum	464
186.	Hypericum punctatum Lam	226
187.	Hystrix hystrix	379, 380, 450, 705
	Hystrix species	370½, 377, 381
	Ilex aquifolium Marsh, see 188	

	Host	*Insects*
188.	Ilex opaca Soland	738, 742
189.	Ilex verticillata tenuifolia Torr	742
190.	Impatiens biflora Walt	706
191.	Impatiens pallida Nutt	706
	Indian currant, see 374	
	Indian hemp, see 31	
	Indigo, see 27	
192.	Ipomea batatas	724
193.	Ipomoea purpurea (L.) Lam	203
	Ipomoea species	436
194.	Iris versicolor L	716
	Ironwood, see 230, 320	
	James sedge, see 84	
	Japanese quince, see 127	
	Jerusalem oak, see 100	
	Jewelweed, see 190	
195.	Juglans cinerea Linn	128, 286
196.	Juglans nigra Linn	128, 227, 228, 286, 392
	Juniper, see 197	
197.	Juniperus communis Linn	415, 443
198.	Juniperus virginiana Linn	419
	Kentucky blue grass, see 271	
198½.	Kalmia angustifolia	217, 392½
	Labrador tea, see 202	
199.	Lactuca scariola integrata Gren. & Godr	726, 743
	Lamb's quarters, see 99	
	Laportea canadensis L., see 395	
	Larch, see 200	
200.	Larix species	363
201.	Lathyrus odoratus ?	726
202.	Ledum glandulosum ?	314
	Leatherwood, see 139	
202½.	Leontodon taraxacum L	719, 740
203.	Lepidium virginicum L	504, 511½, 513, 514
204.	Lespedeza capitata Michx	296
	Lespedeza species	254, 522
	Lettuce, see 199	
	Linden, see 380	
205.	Liquidambar styraciflua Linn	196, 725, 728
206.	Liriodendron tulipifera L	197, 535½
206½.	Lobelia cardinalis L	725, 728
	Locust, see 320	

	Host	*Insects*
207.	Lonicera sempervirens L.	303, 352
208.	Lonicera xylosteum L.	745
	Lonicera species	269
209.	Lupinus albicaulis ?	745
210.	Lycopsis arvensis L.	725
	Lysimachia lanceolata Walt., see 371	
211.	Magnolia tripetala L.	199
	Magnolia species	308, 463
	Maize, see 409	
	Mallow, see 214	
	Malus coronaria L., see 212	
212.	Malus fragrans Rehder	176
213.	Malus malus L.	143, 176, 190, 210, 321, 361, 370, 400, 418, 523, 524, 532, 534
214.	Malva rotundifolia L.	724, 726
	Manna grass, see 234	
	Maple, see 3	
	Meadow rue, see 377	
215.	Medicago sativa L.	725, 726, 728, 734
216.	Meibomia dillenii Darlington	504
	Meibomia obtusa, see 418	
217.	Meibomia viridiflora (L.) Kuntz	296, 504
	Meibomia species	235, 254, 257
218.	Melilotus alba Medic	726
	Milkweed, see 42	
	Millet, see 241	
	Mock orange, see 253	
	Morning glory, see 193	
	Mustard, see 78, 346	
219.	Myrica carolinensis Mill	136, 336
220.	Myrica cerifera L.	132, 223
	Myrica species	136
	Myrtle, see 219	
221.	Nepeta cataria L.	710, 744
	Nettle, see 351, 394, 395	
	New England aster, see 50	
222.	Nicotiana rustica L.	407
	Nicotiana species	726
	Ninebark, see 228	
223.	Nyssa multiflora Wang	135, 389

	Host	*Insects*
224.	Nyssa sylvatica Marsh	134, 389
	Oak, see 100, 293	
	Oats, see 56	
224½.	Ocimum basilicum	724
	Oenothera species, see 412	
225.	Onopordum acanthium L.	766
226.	Onosmodium species	238, 736s
227.	Opocynum cannabinum L.	31
228.	Opulaster opulaster (L.) Kuntz	137
228½.	Opulaster opulifolius (L.) Kuntz	137
229.	Opuntia species	250, 495
	Orache, see 54	
	Orange, see 112	
	Orchard grass, see 133	
229½.	Osmoriza claytoni	736s
230.	Ostrya virginiana (Miller) Koch	119, 128, 138, 308, 315, 328, 334, 335, 354, 364, 396, 440,
	Oxeye, see 172	
232.	Oxycoccus macrocarpus (Ait.) Pursh	140, 395
233.	Oxydendrum arboreum (L.) D. C.	298
233½.	Pachystima myrsinites	468
	Palmetto, see 421	
234.	Panicularia nervata (Willd) Trin	376
235.	Panicum capillare L.	520, 734
236.	Panicum clandestinum L.	434, 456
237.	Panicum commutatum Schultes	722
238.	Panicum dichotomiflorum Michx	734
239.	Panicum dichotomum L.	436
240.	Panicum macrocarpon	526
241.	Panicum milaceum L.	722, 734
242.	Panicum sanguinale (L.) Scop	722, 734
	Panicum species	382, 383
243.	Papaver medicinale	752
	Parsnip, see 173	
244.	Parsonia petiolata (L.) Rusby	431
	Parsonia petiolata Koehne, see 244	
245.	Paspalum dilatatum Poir	718
246.	Pastinaca sativa L.	703, 736, 737, 740
	Pea, see 88, 265	
	Peach, see 28	
	Pear, see 291	
	Pecan, see 177	
	Pepper grass, see 203	

	Host	Insects
246½.	Perezia thurberi Gray	521
	Perilla basilicum, see 224½	
	Persimmon, see 138	
247.	Petasites niveus	401
	Petasites officinalis Moench., see 248	
248.	Petasites petasites (L.) Karst	753
249.	Phalaris minor Retz	734
250.	Phaseolus lunatus L	714
251.	Phaseolus pauciflorus Benth	296
252.	Phaseolus vulgaris L	724
	Phaseolus sp	525
253.	Philadelphus grandiflorus Willd	720
	Philadelphus coronarius L., possibly 253	
254.	Phleum pratense L	705, 722, 734
255.	Physalis virginiana Mill	409
	Physalis viscosa L., see 255	
	Physocarpus opulifolius (L.) Maxins., see 228½	
256.	Picea mariana (Mill)	420, 420½, 459
257.	Picea species	413
258.	Pilea species	438
	Pigweed, see 21, 99	
	Pine, see 259	
259.	Pinus murrayana	416
260.	Pinus ponderosa Dougl	421
261.	Pinus rigida Mill	408
262.	Pinus scopulorum	417
263.	Pisonia obtusata	425
264.	Pisonia oculeata	426
265.	Pisum sativum L	726, 737, 740, 751, 752
	Pitch pine, see 261	
	Plane tree, see 268	
266.	Plantago lanceolata L	748, 750
267.	Plantago major L	516, 720, 737, 740, 748, 750
	Plantago species	726
	Plantain, see 266	
268.	Platanus occidentalis L	117, 141, 142
269.	Platanus racemosa	265
	Platanus species	185
	Plum, see 284	
270.	Poa compressa L	450
271.	Poa pratensis L	381, 734
272.	Poa sylvestris Gray	371, 384
	Poison ivy, see 318, 319	

	Host	*Insects*
273.	Polemonium reptans L.	360, 489
	Pondweed, see 282	
	Popular, see 274	
274.	Populus alba L.	338
275.	Populus angustifolia James	535
276.	Populus balsamifera L.	346
277.	Populus carolina ?	733
278.	Populus carolinensis Moench	144
	Populus deltoides, see 278	
279.	Populus fremontii	606
280.	Populus tremuloides Michaux	351
	Populus species	185, 200, 233½, 400, 453, 501, 503, 507, 510
281.	Portulaca oleracea L.	615
	Portulaca species	747
282.	Potamogeton amplifolius Tuckerm	755
	Potato, see 354	
283.	Prenathes canadense ?	703
	Prickeley lettuce, see 199	
	Prickly pear, see 229	
284.	Prunus americana Marsh	110, 159, 295
285.	Prunus cerasus L.	610
285½.	Prunus melanocarpa	474
286.	Prunus persica L., see 28	
286½.	Prunus pennsylvanicus	226½
287.	Prunus serotina Ehrh	110, 215, 295, 339, 365, 400, 746
288.	Prunus virginiana L.	532
	Prunus species	143, 145, 284, 365, 418, 427, 442, 614
289.	Psedera quinquefolia L. (Greene)	192, 384½, 725, 728
	Psedera species	202
290.	Ptelea trifoliata L.	146
	Purslane, see 281	
	Pussley, see 281	
	Pussy willow, see 335	
	Pyrus arbutifolia (L.), see 41	
291.	Pyrus carolina ?	400
292.	Pyrus communis L.	116
	Pyrus coronaria L., see 212	
	Pyrus malus L., see 213	

	Host	*Insects*
	Pyrus species	215, 295, 418, 534
	Quercus acuminata Michx., see 303	
293.	Quercus agrifolia Nee	166, 270, 481
294.	Quercus alba L.	177, 150, $209\frac{1}{2}$, 291, 302, 308, 329, 337, 355, 527
295.	Quercus bicolor Willd.	123, 271, 293, 297, 301, 307 337, $466\frac{1}{4}$
296.	Quercus castanea	307
297.	Quercus coccinea Wang.	129
298.	Quercus densiflora echinoides Sargent	316
$298\frac{1}{4}$.	Quercus gambelii	$466\frac{1}{2}$
$298\frac{1}{2}$.	Quercus hypoleuca	480
299.	Quercus ilicifolia Wang.	242, 297
300.	Quercus imbricaria Michx.	267, $466\frac{1}{4}$
301.	Quercus macrocarpa Michx.	271, 301, 320, 337, 607
302.	Quercus merilandica Muench.	160
303.	Quercus muhlenbergii Engelm.	329
304.	Quercus nigra L.	271
305.	Quercus palustris Du Roi	104, 123, 158, 160
	Quercus platanoides, see 215	
306.	Quercus prinus L.	240, 307
307.	Quercus rubra L.	129, 160, 325, 329, 341, 441, 527, 730
308.	Quercus velutina Lam.	160
309.	Quercus virginiana Mill.	293
	Quercus species	101, 106 113, 142, 156, 165, 170, 171, 172, 173, 174, 180, 183, 184, $203\frac{1}{2}$ 236, 237, 239, 278, 281, 282, 284, 287, 300, 324, 335, 340, 342, 344, 364, 366, $397\frac{1}{2}$, 444, 462, $466\frac{1}{4}$, $466\frac{1}{2}$, $466\frac{3}{4}$, $471\frac{1}{2}$, 501, 503, 531
	Quince, see 128	
	Radicula armoracia (L.), see 39	

Host	Insects
310. Radicula species	710
Radish, see 40, 311	
Ragweed, see 23	
Rape, see 71	
311. Raphanus sativus L.	726, 751, 752
Raspberry, see 326	
312. Rhamnus californica	147
313. Rhamnus lanceolata Pursh	152, 244
314. Rhodendron albiflorum	188
315. Rhodendron maximum L.	189
316. Rhodendron occidentale	188, 224, 230
317. Rhus copallina L.	231
318. Rhus radicana L.	153
319. Rhus toxicodendron L.	153, 231, 306
Rhus species	127
319½. Ribescereum	487
320. Ridania alternifolia (L.) Kuntz	260, 262
321. Robinia hispida L.	257, 333, 343
322. Robinia neomexicana	469, 523
323. Robinia pseudo-acacia L.	305, 333, 343, 523, 527, 531,
Robinia species	525
Rock cress, see 35	
Roripa, see 310	
Rosa carolina, see 412	
Rosa lucida, see 325	
324. Rosa setigera Michx.	154
325. Rosa virginiana Mill.	154
325½. Rosa woodsii	465
Rosa species	181
Rose bay, see 315	
326. Rubus frondosus Bigelow	155, 168
327. Rubus idaeus L.	713
328. Rubus occidentalis L.	167
329. Rubus odoratus L.	713
Rubus species	360, 602, 603, 604, 605, 713
330. Rudbeckia laciniata L.	248
331. Rudbeckia laciniata flore-pleno	724
332. Rumex acetosa L.	770
333. Rumex crispus L.	515, 764, 765, 768, 769
Rumex hymenosepalus, see 417	

	Host	Insects
334.	Rumex obtusifolius L.	515, 764, 765, 768, 769
	Rutabega, see 70	
	Rye, see 343.	
	Sabal serrulata, see 421	
335.	Salix discolor Muhl.	125
336.	Salix lucida Muhl.	535
337.	Salix pentandra L.	535
	Salix species (see also 414, 415, 416)	139, 185, 189½, 233½, 251, 258, 276, 346, 347, 348, 399, 484
338.	Sambucus species	745
338½.	Sassafras officinale, see 339	
339.	Sassafras sassafras (L.) Karst.	232
	Sassafras species	535½
	Saw Brier, see 349	
340.	Scirpus atrovirens Muhl.	375, 378, 410
341.	Scirpus fluviatilis (Torr)	506, 733
341½.	Scirpus paludosus	485, 491
	Scirpus sp.	375½
	Scotch thistle, see 225	
342.	Scutellaria versicolor Nutt.	233
342½.	Scutellaria latifolia	407½
343.	Secale cerale L.	726, 734
	Sedge, see 82	
344.	Senecio cruentus	740
	Sensitive pea, see 88	
345.	Sericocarpus asteroides (L.)	519
	Service berry, see 26	
	Setaria viridis, see 98	
	Shad bush, see 26	
345½.	Sideroxylon pallidum	195
346.	Sisymbrium officinale (L.) Scop.	726
347.	Sisymbrium thalianum (L.) S. Gray, see 372	
	Skullcap, see 342	
348.	Smilax glabra	252
349.	Smilax glauca Walt.	252
350.	Smilax hispida Muhl.	252
	Smilax species	186
	Snake root, see 15	
	Snowberry, see 373	
351.	Solanum carolinense L.	405, 752
352.	Solanum dulcamara L.	523

	Host	*Insects*
353.	Solanum melongena L.	405
354.	Solanum tuberosum L.	407, 537, 725, 726
355.	Solidago altissima L.	724
356.	Solidago bicolor L.	710, 725
357.	Solidago caesia L.	519, 710, 723, 725, 737
358.	Solidago californica	517½, 724
359.	Solidago canadensis L.	518, 519, 710 723, 724, 725
360.	Solidago flexicaulis L.	710, 723, 725
361.	Solidago juncea Ait.	519, 710, 724, 725
	Solidago laevigata Ait., see 364	
362.	Solidago lanceolata	518
	Solidago latifolia, see 360	
363.	Solidago nemoralis Ait.	725, 737, 740
364.	Solidago sempervirens L.	518
365.	Solidago serotina Ait.	710
366.	Solidago virgaurea	710
	Solidago species	182, 207, 209½ 263, 403 483 488
367.	Sonchus asper (L.) Hill	708
368.	Sonchus oleraceus L.	726
	Sorrel, see 332	
	Sorrel tree, see 233	
	Sow thistle, see 368	
	Spear grass, see 270	
368½.	Sphaeralcea grossulariaefolia Ryds	520½
	Spinach, see 369	
369.	Spinacia oleracea	726, 762, 766
370.	Spirea species	220
	Spleenwort, see 79	
	Spruce, see 257	
	Squirrel-tail grass, see 180	
	St. John's wort, see 185	
371.	Steironema lanceolatum (Walt) Gray	319
372.	Stenophragma thaliana (L.) Celak	752
	Sticktights, see 65	
	Strawberry, see 157	
	Sumach, see 317	
	Sunflower, see 168	
	Swiss chard, see 57	
	Sycamore, see 268	

	Host	*Insects*
388½.	Tsuga species	413
	Tulip, see 206	
	Turnip, see 70	
	Typha latifolia, see 413	
389.	Ulmus alata Michx.	534
390.	Ulmus americana L.	107, 279, 358, 501, 534, 609, 729
391.	Ulmus fulva	107, 164, 279, 358
	Ulmus racemosa Thoms, see 392	
392.	Ulmus thomasi Sargent	107, 164
	Ulmus species	330, 609
393.	Umbellularia californica Nuttal	357
	Umbrella tree, see 211	
	Umbrellawort, see 15	
394.	Urtica gracilis Ait	523, 727
395.	Urticastrum divaricatum (L.) Kuntz	727
396.	Vaccinium ovata	327, 220½
	Velvet leaf, see 2	
397.	Verbena species	723, 724
398.	Verbesina alternifolia, see 320	
399.	Verbesina virginica L.	262, 264
	Vetch, see 401½	
400.	Viburnum dentatum L.	359
401.	Viburnum prunifolium L.	369
401½.	Vicia species	476
402.	Vigna repens (L.) Kuntz	714
403.	Vigna sinensis (L.) Endl	734
404.	Vigna ungiculata	726
405.	Viola species	723, 606½
	Violet, see 405	
	Virginia creeper, see 289	
405½.	Vitis arizonica	390½
406.	Vitis cordifolia Michx.	390
	Vitis species	190, 201, 202, 384½, 388, 390, 442
	Walking fern, see 80	
	Walnut, see 195	
	Watermelon, see 113	
	Wax weed, see 244	
	Wheat, see 386	
	Wild carrot, see 135	

	Host	Insects
	Wild columbine, see 33	
	Wild lettuce, see 199	
	Wild parsnip, see 246	
	Willow, see 335	
	Wingstem, see 320	
	Winterberry, see 188	
	Wire grass, see 142	
	Witch grass, see 235	
	Witch hazel, see 167	
	Wood nettle, see 395	
407.	Xanthium canadense Mill.	717, 728
408.	Xanthium strumarium L.	724
	Yard grass, see 142	
	Yellow rocket, see 78	
409.	Zea mays L.	709, 721, 722, 726, 728, 734
410.	Zinnia species	724
411.	Cercocarpus ledifolius	486
412.	Rosa carolina	467
412.	Oenothera species	428
413.	Typha latifolia	492, 493
414.	Salix gendleriana	535
415.	Salix exigua	535
416.	Salix schouleriana	535
417.	Rumex hymenosepalus	538
418.	Meibonia obtusa	504
419.	Cucumis species	537
420.	Curcubita species	537
421.	Sabal palmetto	496
422.	Sabal serrulata	496

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Sans Tache

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SANS TACHE
BALTIMORE

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IN THE "elder days of art" each artist or craftsman enjoyed the privilege of independent creation. He carried through a process of manufacture from beginning to end. The scribe of the days before the printing press was such a craftsman. So was the printer in the days before the machine process. He stood or fell, as a craftsman, by the merit or demerit of his finished product.

Modern machine production has added much to the worker's productivity and to his material welfare; but it has deprived him of the old creative distinctiveness. His work is merged in the work of the team, and lost sight of as something representing him and his personality.

Many hands and minds contribute to the manufacture of a book, in this day of specialization. There are seven distinct major processes in the making of a book: The type must first be set; by the monotype method, there are two processes, the "keyboarding" of the MS and the casting of the type from the perforated paper rolls thus produced. Formulas and other intricate work must be hand-set; then the whole brought together ("composed") in its true order, made into pages and forms. The results must be checked by proof reading at each stage. Then comes the "make-ready" and press-run and finally the binding into volumes.

All of these processes, except that of binding into cloth or leather covers, are carried on under our roof.

The motto of the Waverly Press is *Sans Tache.* Our ideal is to manufacture books "*without blemish*"—worthy books, worthily printed, with worthy typography—books to which we shall be proud to attach our imprint, made by craftsmen who are willing to accept open responsibility for their work, and who are entitled to credit for creditable performance.

The printing craftsman of today is quite as much a craftsman as his predecessor. There is quite as much discrimination between poor work and good. We are of the opinion that the individuality of the worker should not be wholly lost. The members of our staff who have contributed their skill of hand and brain to this volume are:

Keyboard: Vera Taylor, Mildred Lambert, Hannah Scott, Helen Twardowicz, Anna Rustic, Laurel Tourtelotte.

Casters: Kenneth Brown, Charles Aher, Ernest Wann, Mahlon Robinson, Martin Griffen, George Smith, Henry Lee, Charles Fick, George Bullinger.

Proof Room: Sarah Katzin, Alice Reuter, Mary Reed, Ruth Treischman, Lucile Bull, Audrey Tanner, Ethel Strasinger, Dorothy Strasinger, Angeline Eifert, Lillian Gilland, Ida Zimmerman.

Composing Room: John Crabill, William Sanders, Arthur Baker, James Armiger, Herbert Leitch, Ernest Salgado, Charles Wyatt, Robert Lambert, John Flanagan, Anthony Wagner, Ray Kauffman, James Jackson, Theodore Nilson, Edward Rice, Richard King, George Moss, Henry Shea.

Press: Leo Ledlich, Clarence Ridgeway, George Lyons, Raymond Bauer, Hugh Gardner, Wm. Harrison, Jr.

Folder: Laurence Krug, Shipley Dellinger.

Cutter: William Armiger.